

ONE-PARENT NESTING IN CINNAMON-VENTED PIHAS (*LIPAUGUS LANIOIDES*, COTINGINAE, TYRANNIDAE)

Edwin O. Willis & Yoshika Oniki

Departamento de Zoologia, UNESP, 13506-900 Rio Claro, S. Paulo, Brazil.

Resumo. Cuidado do ninho por um adulto em cricrió-suisso (*Lipaugus lanioides*, Cotinginae). Dois ninhos de cricrió-suisso das matas serranas do Espírito Santo, Brasil, mostraram que o comportamento anti-predador pode auxiliar na explicação de não monogamia. Contrário à idéia que a frugivoria ocasiona promiscuidade, a espécie é um tiranídeo de pernas curtas, alimentando-se de insetos grandes como gafanhotos e louva-a-deus assim como frutos; a maioria do alimento trazido para o filhote era insetos. A evolução para o uso de níveis médios escuros e abertos da floresta, com movimentos em cadeia atrás de alimento, pode ter forçado os cricriós a abrirem mão da territorialidade do macho (locais de frutificação sendo mutáveis, as brigas perigosas e a detecção de oponentes difíceis) e a guarda do par (seguindo ou chamando-a, perigoso e a detecção da fêmea camuflada difícil), parcialmente devido à presença de gaviões que caçam por tocaia. Assim, os dois métodos principais de prevenção de cópulas extra-par tornaram-se difíceis, enquanto os machos não eram apenas emancipados do cuidado do ninho mas atacados pelas fêmeas porque eles exploram o alimento ou atraem predadores próximos ao ninho. Um filhote silencioso e imóvel auxilia a evitar os predadores embora eliminando as vantagens da ajuda do macho. Períodos de incubação e de criação no ninho longos (25–26 dias) e visitas dispersas permitem aproximações lentas e cuidadosas pela fêmea. Talvez a ajuda do macho não auxiliaria em encurtar o desenvolvimento do jovem tiranídeo que precisa voar bem ao sair do ninho devido às pernas curtas. Sagüis e aves, possíveis predadores foram atacados, assim como aves pequenas e o macho em todas as ocasiões. A fêmea foge com o passar de aves grandes ou fica esperando até 36 minutos com um grande ramo ou inseto-pau no bico durante a aproximação ao ninho. Ela é silenciosa, exceto pelo barulho das asas quando atacando um grande arapaçu próximo ao ninho ou notas “bafejadas-rápidas” para chamar o filhote para fora do ninho. O jovem tem penugem alaranjado e assemelha-se à uma taturana “cabeluda”, depois torna-se amarronzado pálido e difícil de se ver, coçando-se apenas na presença da fêmea. O jovem e a fêmea no sol, ou com a poeira vindo da estrada, ficam se coçando ou abrindo o bico, indicando que o verão quente e seco (efeito estufa?), mais às margens da floresta com a abertura de estradas e o desmatamento podem afetar a nidificação de espécies adaptadas para as matas úmidas de altitude. É necessário que os estudos dos efeitos de borda sejam estendidos para englobar outras áreas como a fisiologia e os estudos de invasões de gaviões que vivem nas bordas.

Abstract. Cinnamon-vented Pihás (*Lipaugus lanioides*, Cotinginae, Tyrannidae) showed antipredator behavior, at two nests in montane forest of Espírito Santo, Brazil, that may help explain nonmonogamy. Contrary to ideas that fruit eating causes promiscuity, the species is a short-legged flycatcher, eating such large insects as katydids and mantids as well as fruits, with most nestling food being insects. Evolution into the open but dark forest midlevels, partly to exploit food by traplining, may have forced pihás to give up both male territoriality (fruit locations being changeable, fighting dangerous, and detection of opponents difficult) and mate guarding (following or calling being dangerous, and detecting the camouflaged female difficult), partly due to a change from fast-moving hawks at edges to sit-and-wait predators in the midlevels. Thus, two main methods of preventing extra-pair copulations became difficult, while males were not only “emancipated” from nest care but “disenfranchised,” attacked by females because they eat food near nests

and attract predators of themselves or nests. A tiny nest and one nearly immobile and silent young help avoid predator detection, but eliminate advantages of male help. Long incubation and nestling periods (25–26 days) spread out visits and allow slow and careful approaches; perhaps male help could not shorten development because feeding rates would increase and because short-legged young Tyrannidae have to fly well on leaving. Marmosets and avian possible predators were attacked, some small birds nearby, as well as yelling male pihás at all times. The female fled at passing large birds and could freeze up to 36 min with large twig or stick-insect in the beak on nest approaches. She was silent, except for a wing-whirr attacking a large woodcreeper near the nest and for “fast-puffing” notes to call the nestling out of the nest after a monkey troop passed. The young has orange down that resembles a hairy caterpillar, then is buffy-dull and hard to see, for it preens mainly when the parent stands near watching. Some preening and gaping of young and female in sun or with road dust indicates that the hot dry summer (greenhouse effect?) of study, plus forest edges with road clearing and Brazilian deforestation, may affect nesting in species adapted to shady humid uplands; study of edge effects should be extended to physiology and to invasions by edge-living hawks. *Accepted 25 January 1997.*

Key words: Cinnamon-vented Piba, *Lipaugus lanioides*, Tyrannidae, Cotinginae, nesting, predation, monogamy, promiscuity, edge effects.

INTRODUCTION

Most birds are monogamous, while most mammals are not. Male mammals cannot feed young, hence increase the number of their offspring mainly by seeking several females; a male bird can feed young, hence can raise a larger brood if he stays with one female. Although some species of temperate-zone birds that are seemingly monogamous engage in extra-pair copulations (EPC's), males help with nesting in the majority of bird species, whether or not EPC's occur. Even polygamous birds, with several mates, often help feed nestlings of one or a few females.

In suboscine tyrant-flycatchers (Tyrannidae), males usually do not incubate, but do feed young. These flycatchers (as well as many songbirds, Oscines) are mainly species of open or semi-open zones, seasonal habitats where the male has to sing and defend territory against territorial or EPC invaders exactly when the female is incubating. Males that help incubate run a risk of EPC's (Riley *et al.* 1995) and lose chances to copulate with outside females. Later in nesting, male help in

feeding young allows larger brood sizes, and there is no longer danger or possibility of EPC's or territorial invasion, so the male can easily help feed offspring (Willis 1995). Large testes in northern and migrant “songbirds” (actually Passeriformes) compared to forest ones perhaps support the idea of EPC's in seasonal habitats (Stutchbury & Morton 1995); but the tyrannids and nonmonogamous tropical birds should have fairly large testes, too.

Certain tyrannids, especially cotingas (Cotinginae) and manakins (Piprinae), live in the forest interior rather than at its edge or in open areas. In many of these forest tyrannids, including such insectivores as *Myiobius* sp. and omnivores as *Mionectes* sp., females care for nests alone, instead of evolving toward male help during incubation or care of nestlings as in many forest birds (Skutch 1960, 1969). Certain forest songbirds also show this pattern of care, notably bower-birds and birds-of-paradise (Paradisaeidae) of the Australian region (Beehler 1983a). Some neotropical woodcreepers (Dendrocolaptidae) (Willis 1972, 1979) also have evolved this pattern, even

though males help with incubation as well as nestlings in related species. Lack of male help with young has also evolved in such nonpasserines as grouse (Tetraonidae), certain sandpipers (Scolopacidae), bustards (Otididae), and hummingbirds (Trochilidae). Often, these males have evolved “lek” or “arena” displays to attract females (Höglund & Alatalo 1995, Johnsgard 1994).

Independently evolved female-only nesting could have few or several causes (see Discussion), links to sex and frugivory having been proposed by several authors (e.g., Snow 1963, Bradbury 1981, Beehler & Foster 1988). We began to suspect that predation may affect monogamy after watching insectivorous nonmonogamous woodcreepers and tyrannids (Willis 1972, 1979, Willis *et al.* 1978, Willis & Oniki 1995), as well as monogamous frugivores (parrots and tanagers; in both these latter cases males follow their mates carefully). Ethologists, living in a world where they rarely are preyed upon, can fail to appreciate the importance of rare predation events in nature and could overemphasize sex and food, two things that do bother humans. A recent study confirms that predation has been overlooked even in well-studied primates (Ron *et al.* 1996).

We had the occasion to study details of one-parent care at two nests of the Cinnamon-vented Piha, *Lipaugus lanioides* (Tyrannidae, Cotinginae), in upland forest of southeastern Brazil. A behavioral analysis may suggest why female pihans and related cotingas care for a single egg and young alone, while males wander or sing loudly in established leks of one or several males, with only one possible case of monogamy (Skutch 1969, Snow 1982).

The Cinnamon-vented Piha is an endemic cotinga with a relatively restricted distribution in upland or subtropical forests of southeastern Brazil, where it replaces the related Screaming Piha (*L. vociferans*), a lek-forming

(several males sing loudly in restricted areas in the forest) species of much wider distribution in the lowlands of eastern Brazil and Amazonia. At 85–110 g, females are slightly heavier than males but smaller in measurements (Snow 1982). With its thrush-like bill but wide pink-yellow gape, the piha looks like a plain gray short-legged thrush. The piha sits somewhat upright like a flycatcher and peers about slowly, sidling or sallying for fruits or insects on limbs or foliage from nearby to several m off. Solitary pihans wander 5 to 25 m up above the ground in the forest shade, occasionally descending near the ground.

Normally silent, the male emits a loud whistle of several notes (“serk-serk, whseek-wserk”) at long intervals, mainly in certain areas in the forest. Irregular series of whistles erupt briefly at times, in these areas or elsewhere. At times, in Nova Lombardia, 2 or 3 males sing rather close together, in an area 100 m in diameter. In 1975, one male sang repeatedly near a tree in fruit, *Rheedea madruno* (Clusiaceae), at Fazenda Barreiro Rico, Anhembi, São Paulo, in a dry interior forest where the species is rare (Willis 1979b). Similar song patterns occur in related bellbirds (*Procnias* sp.) and many other cotingas, in some of which the male has bright plumage or joins other males in “leks” to display or sing.

C. Balchin (pers. comm.) and his group found a thin nest of sticks, 7 m in a tree by the road in Nova Lombardia, on 28 December 1993. The adult went on the nest, apparently incubating. At another place, a grown fledgling seemed to beg for food (C. Balchin & N. L. Goodgame, pers. comm.). Nesting seems to take place from September to March, according to these and our own records.

METHODS

We studied breeding and other behavior at

two piha nests about 2 km apart in January–March 1995, along roads at 850 m elevation through upland forests of the Reserva Biológica Augusto Ruschi or (formerly) Nova Lombardia, Espírito Santo, Brazil, at about 19°54'S and 40°33'W. Forests are 20–35 m tall, with many epiphytes, and much rain and clouds in normal summers (1995 was unusually hot and sunny, the roads becoming dusty). T. A. de Melo Jr. and A. Z. Antunes, student assistants, made some of the observations in mid-January; Willis and Oniki made all others. Times registered here are standard time. We watched from roads 10 m S of the first nest and 15 m S of the second, without using blinds, for the females seemed to ignore us. A third nest, 7 m up in a tree on the road, was briefly watched on 31 December 1995.

RESULTS

Nest building. Our nest-1, a thin platform 8 m up, already had one egg when we found it on 19 January 1995. A single bird, presumably female, was building our nest-2, at 13:55 on 24 January 1995. Jon Hornbuckle and other observers (*in litt.*) had seen her carrying twigs nearby earlier that day. A few thin twigs, some 8 m up on a twig and side twig, resembled the barely more substantial nest-1. Both nests were in slightly cluttered twigs and small vines, well above the ground and well below the canopy, in the open lower midlevels of the forest, somewhat below normal foraging levels.

The building female made 9 visits in 1 h, vanished for 50 min and visited 3 times from 15:52 to 16:05, then once at 17:40, with no more visits before Willis left at 18:33. On the 25th, between 06:29 and 11:15, there were visits at 06:30, 06:54, five from 07:26 to 07:57, others at 08:55, 09:31, 09:57, 10:11 and 10:55, showing the irregular bouts noted the first afternoon. On the 27th, from 08:16 to 11:32 and 15:35 to 16:15, she visited only at 08:27,

08:44 and 09:06. On the 29th, from 06:48 to 10:48, she visited at 06:59, 07:10, 07:36 and 09:20. There were no visits on January 31 (from 06:37 to 09:37) nor on 1 (08:05 to 10:19) or 2 February (06:29 to 08:57). On the 3rd, she was incubating a single egg (07:08 to 09:22). Thus, building the tiny nest plus waiting for an egg took at least 11 days, for the nest was large enough on the 24th that it had probably been started on the 23rd or earlier.

Slow or sudden movements were characteristic of nest approach. With the middle of a thin twig crosswise in the bill, the female watched 1 or more min per perch, then dove quickly to the next one, finally to behind the nest or to the nest itself. At each perch, she turned her head slowly or bowed and scraped 90° while watching; she could reverse 180° suddenly, or fly to a perch just past the nest, with tail toward it, reversing suddenly after a long pause to hop to the nest.

Certain perches were used more than others, but none in any regular fashion except the perch just behind the nest, which was used often for the “final reversal.” Approach took more stops and time on the first visit after a long interval; the visits at 15:52 and 17:40 on 24 January and at 08:55 on 25 January were very cautious. It is easy to miss a move if one blinks, especially when the bird arrives from a distance and one’s attention has lapsed slightly. On the 09:31 visit, the female took 8 min to approach the nest, stopping at 3 perches, plus 1 min on the perch next to the nest. For the 06:59 visit, apparently watching a noisy canopy flock of parrots (*Pionus maximiliani*), she waited 11 min on a single perch with a twig in her beak.

When the female hops up on the nest, she waits several seconds to a minute before quickly depositing the twig. She can fly off immediately, or sit and work, perhaps turning several times and pushing or pulling twigs, or pressing down on the slight nest with foot movements one to several times. She waits,

puts, waits, pushes, tramples, waits, sits, pulls, waits. She pecks to remove nearby dead leaves or moss at times. Once she dove after a falling twig, catching it 5 m below the nest and returning to 2 m below the nest, then to work again. Once, she descended 0.5 m to get a fallen twig and return it to the nest, and once dove 0.3 m as if after something, returning. A large twig took 19 min of work on the 10:55 visit, and other visits were (1–8 min; 1 min = 9 visits, 2 min = 4, etc.) 9-4-5-4-5-1-1-2.

The piha flew rapidly 10 m or more from the nest each time she left. After an initial slight drop she rose into the subcanopy, with more foliage, on distant flights; and rose going N or uphill on short flights, while short flights downhill (or S to near Willis) ended up some 10 m above the ground, near the nest level. For short trips looking for material, she went SE to SSW 10 times, N 5 times in a row on 24 January and W 3 times. She never went E past the trunk of the nest sapling. For long intervals away, she went far N to W on 9 occasions, S only twice.

For short trips, intervals away from the nest were 2-1-3-4-1-1-0-1-2-1 (for 1–10 min away), with 17–99 min away for long trips. To get dead slender twigs, she looked up and around at a few perches, sallying upward or sidling along a branch to peck. If the material came off, she moved her mandibles back and forth to center it in the bill, flying then toward or to the nest. One twig was longer than her length. In one case, she looked from 3 perches in 3 min about 15–20 m from the nest, darted off further and returned with material 2 min later. After 4 min on the nest, she hung and fluttered on several sallies for twigs over the road 15 m S of the nest for 4 min, gave up and left for 45 min, then visited over 1 min at 2 m from the nest before to the limb behind it for a “reversal” (total time off, 50 min). Once she “chewed” a twig but dropped it, without diving to retrieve. In

other cases, pulling and fluttering at several spots failed to loosen tough vine tendrils.

On 27 and 29 January, she brought mostly small tendrils for the lining instead of the long twigs carried earlier; trampling under her was infrequent, and she sat and preened briefly.

Incubation. We watched incubation at nest-1 for a total of 66.9 h (January 19–30 except 23, 26 and 28). At nest-2, we watched incubation 3 to 28 February for a total of 171.6 h (125.5 h from 18 to 28 February; no observation on 5, 8, 11, or 13 February).

When incubating, the female sits somewhat upright as if she were on a perch; the nest is barely visible and her tail sticks far out. However, there is no persistent movement as if “foraging,” as noted for another cotinga, *Iodopleura pipra* (Willis & Oniki 1988), and the female is not as upright as she would be normally; there is no evidence that she is mimicking an active bird standing on a perch and not on the nest. Crypsis depends mainly on the tiny nest and the usual lack of female movement. At night, however, she took very low postures as in *I. pipra* and other incubating birds.

The piha may move her feet, perhaps turning the egg, with or without rising. Sometimes she yawns. She mostly looks around very slowly, occasionally standing and turning. She may preen busily for short periods, including several times when wind ruffled understory leaves.

The lower sun of late summer started to hit the female at nest-2 at certain hours, causing her to open the beak, fidget and preen, turn on the nest and leave after unusually short incubation sessions, twice on the morning of 22 February. On sunny 23 February, she seemed undisturbed while, on 24–25 February, she stayed incubating for long periods in the morning (despite sun) but, after noon (despite shade), she seemed itchy (preening

often) and hot (beak open); there were sequences of rather short incubation sessions during both afternoons. From 26 February on, cloudy mornings left her less itchy, and incubation sessions were near the median (46 min, see below). The female at nest-1 often had the beak open when sun hit her, as on the hot midday of 27 January. A dark understory bird like the piha cannot, apparently, stand much sunlight even if it is only a passing sun-fleck.

The female at either nest could stretch both wings over the back ("two-wing-half-flex") as in normal preening. At times she regurgitated a seed, which fell below the nest with an audible click. Frequent preening on the nest may have been affected by molt. The female at nest-2 was recognizable by tail molt, the two central feathers growing slowly (2/3 length on February 27, plus primary 5 from the outside on the left wing 1/2). She lost another primary the day the young hatched, and central tail feathers were still 4/5 of normal length by March 18, perhaps due to interrupted molt (but molt is slow in Cotinginae; Snow 1976, 1982). The female at nest-1 lost one body feather while preening in late January.

On 18 February, from 10:00 to 11:00 h, *Azteca*-type ants (not army ants; Willis checked) ran the female off the nest. She pecked them from the nest edge and pulled at twigs, with shakes of the tail, especially from 10:17 to 10:26 when they finally ran her off. She once rolled the egg up to her chest; fortunately it was not broken. She tried to return and peck at 10:35 and 10:53 but fled; at 11:02 she finally sat after many pecks. She pecked less often, left from 11:31 to 11:48, and pecked infrequently thereafter.

Once the first female, and three times the second, left the nest abruptly to attack another piha 6–30 m off, the three latter cases probably males as they yelled loudly in fleeing. The female was silent, except for a whirr of

wings. These three cases were after a melastome tree 15 m off came into fruit. Once the second female watched the other piha high in the melastome for several minutes before attacking it, for she had to climb abruptly after an initial dive off the nest as if to gain speed. She fed and preened in the melastome herself on a few occasions. She mostly ignored *Chiroxiphia caudata* and other rare visitors in the melastome. The first female, however, once attacked *C. caudata* near the nest and once in a melastome tree near it. Once she also attacked an *Automolus leucophthalmus* that sang near the nest, and once an unidentified small bird near it.

On 27 February at 11:07, the female left nest-2 and flew up to attack a much larger hawk (*Harpagus diodon*) that alighted in her melastome. It fled past the nest tree to over Willis 15 m S, where it looked back as if not sure what had happened, then flew off S. At 14:08 on 26 February, she did not move when a forest-falcon (*Micrastur ruficollis*) flew to 4 m up between Willis and the nest; it bobbed the head and chuckled at him several times, and finally, flew off low SW across the road. Both incubating females seemed to watch the upper levels of the forest, perhaps looking for hawks. As a branch fell or a fast shadow passed overhead, either female sometimes flattened out and stuck the head forward, or lifted one or both wings briefly. Closing a car door, and a distant passing trogon, caused her to leave the nest briefly on separate occasions, though she ignored passing cars and resulting dust swirlings, as well as a small woodcreeper (*Sittasomus griseicapillus*) near the nest.

The female fled nest-2 instantly when a passing pigeon (*Columba plumbea*), a fair-sized parrot (*Pionus maximiliani*), and (after 31 min on, perhaps normal) a small unidentified bird rapidly passed at or near the level of the nest. Once she left, less abruptly, when a *Trogon* cf. *sarrucura* flew high overhead. On most occasions she ignored approaching bird flocks,

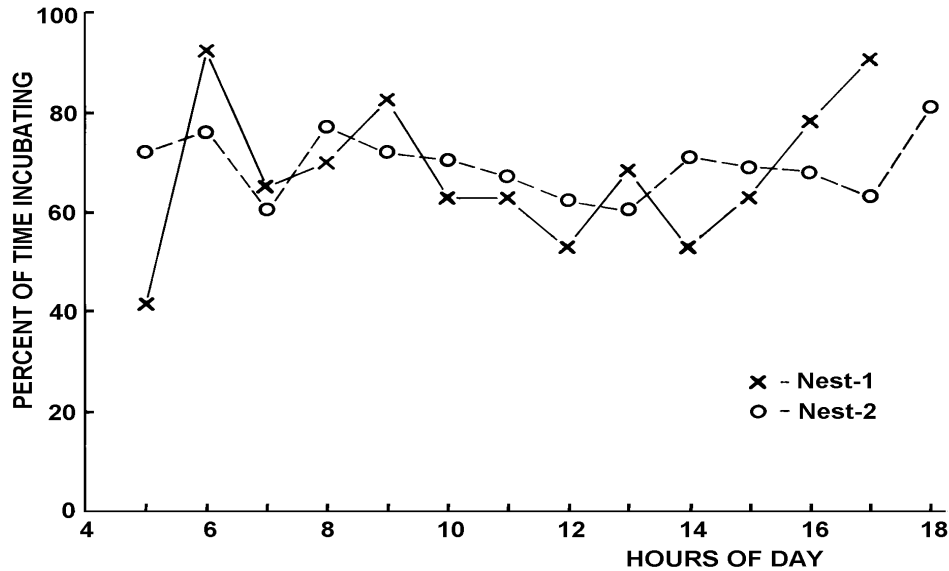


FIG 1. Percent of time incubating at different hours of the day at two nests.

but on others she left the nest (once after an unusually short 14-min incubation) for a time. She often returned before the flock moved on. However, at 06:41 on 9 February, she spent much of 86 min off the nest following and watching a pair of toucanets (*Selenidera maculirostris*), which are possible nest robbers, foraging through the leafy upper understory not far above the nest and 25 m W of it. On 28 February, from 11:05 on, she stayed off the nest nearly an hour as an understory flock approached and passed, and a pair of large woodcreepers (*Xiphocolaptes albicollis*) moving with the flock searched all trunks up to the level of the nest. The female had moved down near the ground, watching them constantly. When one woodcreeper finally was climbing a trunk 0.5 m from the nest sapling and 0.5 m below, at 11:48, she opened her tail, flitted her wings, bowed and scraped from one side to the other from a horizontal twig below the nest, and drove the woodcreeper off with a loud whirr of wings.

She let the two move off SE with the flock, then went on the nest at 12:02. On 7 February, she had been sitting and ignored the bird flock and a single woodcreeper at 07:41, though it pecked at moss on the trunk barely 1 m below the nest.

All five species of monkeys in the reserve passed by the nests during our studies. Even though noisy, distant (*Brachyteles arachnoides*) or high (*Callicebus personatus*) groups seemed to be ignored. Nearby, a silent but jumping *Alouatta fusca* duo caused certain effects during the nestling period (below). Near noon on 23 February, an approaching large troop of *Cebus apella*, working from the level of the nest on up, apparently caused the female to leave nest-2 twice for short 9- and 14-min intervals, and stay for 19- and 23-min short sessions, before she returned slowly to the nest. A second passage of these monkeys is detailed below, for it caused the female to call the grown nestling out of the nest. At nest-3, on 31 December 1995, *C. apella* fled nearby

when Willis and students came up, and the female gradually moved to incubate. A group of marmosets (*Callithrix flaviceps*) at nest-1 caused even more trouble (below).

The female stopped incubating twice for a sudden sally after cicadas near nest-2, once for a successful 3-m horizontal sally, and once for an unsuccessful one of about 7 m (5 m out and 5 up, “5 + 5” in our notes), plus another chase of an unidentified insect.

The female left nest-2 when still nearly dark, between 05:40 and 05:51, for a brief sortie (6–14 min), probably to get fruit in some fruiting tree or to preen and defecate. In the evening, however, she normally returned between 17:15 and 18:06 (mean, 17:45) long before dark which occurred at 18:30. However, she was frequently absent from the nest between 17:00 and 17:45 for “dinner”. She was also off the nest more for “breakfast,” between 07:00 and 08:00 h, and “lunch,” near noon (Fig. 1). We have previously found this pattern in other tropical birds (Oniki *et al.* 1992, 1994).

The first female had a different schedule, for she arrived at the nest for the night between 16:15 and 17:28 (mean 16:50), except when she left to attack some bird on the ground (*Grallaria varia* or the like) at 17:24 and 17:43, returning at 18:15. She was often off the nest around 06:00–07:00 and 08:00–09:00, also 11:00–14:00, as if on a “2 meals a day” schedule. Of course, dawn was earlier in January, but dusk was also later.

Intervals off nest-2 (not counting long incidents with ants, toucanets, or woodcreepers, a brief 3 min off to attack the hawk, nor 7 or 20 min when scared by passing birds, nor brief intervals at dawn) ranged from 9 to 50 min. The median of 111 cases was 18 min, the peak 16–20 min (41 records).

Longer intervals off were all the first week or so of incubation, shorter intervals all late in incubation, except for 33 and 35 min for “dinners” on two days late in incubation. The

shortest early interval was 17 min, the longest intervals late were 30 and 33 min, not counting evening meals. Only on 3–4 February, as incubation started, were there intervals of 32, 34, 48 and 50 min. A dinner on 10 February lasted 38 min.

Intervals off nest-1 (not including midafternoon “dinners” of 47 min after attacking a piha nearby and 48 min with a circuitous 22-min approach) ranged from 12 to 34 min, with a major peak of 26–32 min and a minor one near 18; the median for 51 cases was 27 min. This female probably had a different foraging system from the second female, with longer trips or stocking up on food so she didn't have to go out in the evening.

Incubation sessions at nest-2 (excluding short ones ending in attacks on other birds or insects, or because of flying bird, sun-fleck, monkey or ant problems) were 12 to 124 min, with 4 periods over 1.5 h early in incubation (2), in late day (1), or midmorning (3, including the 2 early in the month). A broad peak of 31–65 min (71 cases) was registered, the median of 102 cases being 46 min.

Incubation sessions at nest-1 (44 records, median of 41 min, excluding 13 and 22 min before attacks on *Grallaria* and *Automolus*) were 23 to 93 min, the latter during midmorning as was one of 91 and another of 76 (the 4th longest was 66, on 22 January just after the 93-min session, on a cool day after a night rain). Oddly, including this case, three of nine sessions exceeding one hour were in the hot afternoon (twice on cool days) even though all ten 23–32 min short sessions were at these hours.

A violent rainstorm, scattering leaves all over, was bending the tree with female on when we fled, late on 22 January. At forest edges and in Santa Teresa, it knocked down trees, but the shallow nest survived, thanks to the windbreak of large forest trees. Even two days later, temperatures were down and after-

noon sessions of the female long.

Before leaving the nest, the female usually looks about more actively, hops up and over the nest edge and dives away to 10 m or more from the nest, rising if she has to go uphill. Once the second female left in the direction of a male song far off S (4 February, 15:46). Songs near or far from nest-1 never interested the incubating female. Series of distant non-song calls in various directions never seemed to interest either female.

Approach to the nest was cautious, and often took much time, as when building. On 70 visits at nest-2, the female arrived without detection, or (38 cases) as she hopped to the nest. On 64 other visits, she preened and moved from one branch to another toward the nest from 1 to 19 min (27-10-4-8-7-2-2-1-0-1-1 up to 11 min, once 19) on the approach, often with a long pause next to and behind the nest with her tail toward it.

At nest-1, slow and devious approaches were also common, the female watching carefully at each stop, reversing at times. Not counting 6 visits when she was entering the nest when detected, records of 1–8 min on the approach were 22-9-6-3-0-1-0-1, plus 3 cases of 10 min and 1 each of 13, 14, 15 and 22 min, for a median of 2 min.

Although it was easier to see the female at nest-1 approach than at nest-2, the first female hardly ever came from S of the road past the observer (tall secondary forest was uphill to the S). On the longest approach, she ate several fruits, hitting them on branches as if they were insects; she circled over Melo, attacked a manakin in “her” melastome, then circled north slowly and back west to the nest. On the next longest approach, she got several fruits in her melastome, preened there, and circled slowly north and back west to the nest. For the 14-min approach, she preened, attacked an unidentified bird, preened, got a 0.5 B (B = one bill length) insect, a melastome berry, and moved in

slowly. She ate melastome berries and circled slowly on 13-min, 10-min and 8-min approaches. On two 10-min approaches, she circled over Melo, preening and looking. She often stopped at certain perches near the nest, but not in any regular pattern. She could reverse next to the nest, her tail toward it, but did not do so as regularly as did the second female. On other slow approaches, she sallied for a brown tettigoniid (katydid) and ate it, got two small winged insects, and a 2B insect.

The second female sometimes foraged and preened on her careful approaches, as well as look, bow, scrape and dart from one perch to another. Once, she beat a green katydid on a branch at 15 m up on a 7-min approach; she sallied and beat a noisy cicada, mandibulating it, on a 4-min run; once she sallied to foliage 15 m from the nest (4 min, mostly waiting for a cloud to pass over the sun and insect noise to stop when next to the nest); once she preened and fled as a car passed (4 min); a sally and preening took 5 min; on another 5-min approach, she sallied and ate a dusty green caterpillar 15 m up; she brought an insect to the egg at 11:19, on 24 February, but ate the prey 1 min after reaching the nest. Once, on a 4-min approach, she bill wiped then sallied to a limb for a white-hairy Homoptera, tried to wipe its hairs off on a branch but released it and wiped her bill busily, then scratched her head over the wing. Wiping the beak was a common activity on approach, as well as other preening. On the 19-min approach, she preened and several times sallied to dewy leaves over the road 15 m S of the nest, shaking and preening after each “bath,” from 06:35 to 06:53 am; then she took 1 min to the nest. Normally, she foraged far away from the nest, but once near noon moved almost to the ground, regurgitating a seed and looking about, 25 m S of the nest and across the road, for 11 min before vanishing for a few minutes enroute to the nest. The 8, 8, 10 and 11-min sessions were

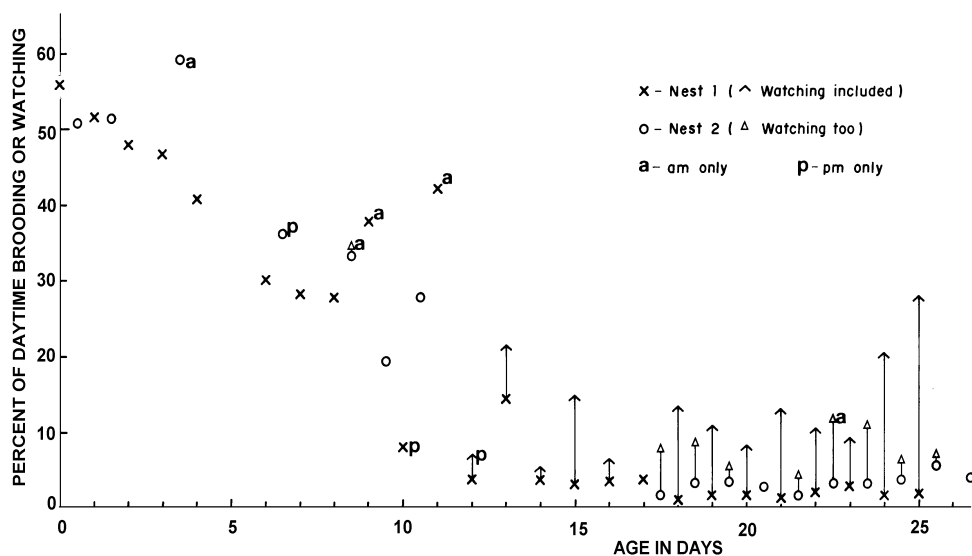


FIG. 2. Percent of day brooding or watching young bird at two nests. In general, morning brooding (a) was more extensive than afternoon (p); watching was more frequent at nest-1.

mostly preening, on favorite perches high over the road and observer, where she could look down toward the nest, late on the afternoons of 23, 25 and 26 February. In one 5-min and a 1-min cases, she preened or sallied in the melastome behind the nest; in another case, she spent the whole 15 min off the nest sallying and preening in the melastome, on her penultimate trip of the day. She also visited the melastome leaving the nest on 5 occasions, although it seemed more in flower than in fruit.

Leaving nest-2, the female often dropped and flew away rapidly, rising into the upper levels and disappearing with wide wing strokes like an oropendola. Once she sallied to foliage enroute, once (at 06:47) defecated S of the nest and turned E (the direction somewhat blocked by the nest tree). On two other departures, she preened 1 and 7 min over the road. Veering 90° or more at 10 or 15 m from the nest was fairly common, 3 times right from a S or SE initial heading, 2 times right

from a SW course, 2 times left from NE, and 2 times left from a S or SE course. Sudden veering in flight is likely to be an anti-predator activity, perhaps concealing the direction of the nest, as we never saw this type of movement elsewhere. She commonly returned in a direction different from the one she had taken leaving the nest, indicating circling about through the forest away from the nest. She went N or NE on 20 departures, NW to WSW on 19, SW to SE on 46, and E on 5 (6 were SE, 7 SSE, and 13 SW). The direction was probably related to her main incubating position, tail N; but she at times reversed on the nest as she left. Direction was not seen in 40 departures. She may also have avoided flying uphill, N to ENE, but this was not as evident as on the steeper slope at the first nest (below).

The first female also veered abruptly to right or left in some flights off the nest, once to the left and four times to the right (one of the latter with a second 90° left turn). She also

returned from a different direction than her departure in several cases, not counting the cases where she circled in the nest area. She flew S over the observer and road only once, going NW on 25 departures, N on 13 and NE on 8; once she went E and once W, along the road. The major problem probably was that the road 10 m S was barely below nest level, so she would have had to fly upward past the observer to end up well above the ground. She also tended to incubate with tail SE, favoring westerly departures, though she did change direction on the nest, even several times in one session. She also barely used the secondary woodlands S and W, or forests upcreek E along the road.

Once she left the nest and egg exposed to a light rain, and stayed away 20 min as the rain slowed and stopped (15:09 to 15:29 on 24 January).

Hatching. Oniki watched the nestling for 237.4 h at nest-1, Oniki and Willis 126.1 h at nest-2. The second nestling hatched after 26 days of incubation, before Willis arrived at 06:36 am on 1 March; he later collected a piece of eggshell from the ground below. The egg is dull brownish with darker spots.

At nest-1, Oniki had noted similar colors as she watched the sitting female bobbing her head, taking 2 min to eat the large half of the shell at 06:52–06:54 am on 31 January. At 06:45, the bird had risen and accidentally dropped part of the eggshell to the ground. Once she flattened out and stretched her head forward as if frightened. Now and then she looked under her or at the ground below. She left at 07:34, returned 9 min later and ate something from the nest, raising her head to swallow it, then settled until 08:13. She half stretched both wings, champed her bill three times, and occasionally shifted on the nest or stood back to look at the nestling, but mostly she was still or looked about slowly from a fluff-bodied and-chinned pose.

She fed the young a tiny dark insect at 08:31, or some two hours after hatching. On her return, she had frozen 3 min on a branch near the nest, then froze 1 min on the nest edge before suddenly bending down to feed. She now stayed brooding for 88 min before feeding the second tiny dark insect after another 3-min approach at 10:21 (not counting time spent on approach before reaching the nest tree).

At nest-2, post-hatching behavior was somewhat less cautious. In fact, the sitting female suddenly sallied twice to a leaf near the nest at 06:47, returned with a tiny insect 06:48, fed the young, and resumed brooding. No food was brought from a brief trip away between 06:53 and 07:00 h, but back from a trip between 07:35 and 07:48 h, she brought a tiny food item after a 2-min freeze on a high perch 19 m off. From 08:10 to 08:33 h, she was off, sallying up short distances to foliage over the road SE of the nest, then off W and (08:30) back with a large green katydid (1B) hidden in her bill. She twice tried to wipe off the long antennae on a branch while waiting 3 min to go to the nest, to feed successfully what must have been a barely larger nestling. Cautious freezing on scattered branches was normal behavior, as was hiding prey inside the beak (see below).

Brooding. As in many other birds, the female ordinarily broods the nestling after feeding it during the first days, then starts to leave after feedings, especially on warm afternoons. Later, she broods only during rains or at night. Later still, the young can be left soaked in rains and the female sits beside it in the evening rather than atop. The female can wait several min next to the young as it preens the last two weeks of nest life, but mounts it only at night (Fig. 2). The female at nest-1 spent more time perched next to her young, allowing it to preen, perhaps for it to remove dust from the road above the nest or for some

other reason. This may have caused her to go on the nest later in the evening and leave slightly earlier in the morning in late nesting. The second female sometimes preened in the nest area several min after leaving the nest, which she watched, but she could not be detected readily.

Until about day 10 (day 0 being the day of hatching), brooding for the night usually began well before dark, near 17:45 as in incubation for the second female (the first female was coming in about 17:45, but later than during her incubation). Dark clouds and fog probably caused a 17:06 record on day 7 at nest-1, rainy weather two other records (one at nest-2) before 17:20, and cool cloudy weather the only other record. Marmosets (*Callithrix flaviceps*) around nest-1 on the afternoon of day 3 (and morning of day 4) suddenly caused a late arrival at 18:21 after two early visits (above), despite clouds and a bit of rain. At nest-2, a late 18:09 entry on day 17 despite clouds was almost certainly caused by two male howler monkeys (*Alouatta fusca*) jumping down into midlevel and upper understory trees in the area late in the day. The female visited the nest very infrequently, late these afternoons, a pattern also noted on two other days (at nest-1) when the female came in well after 18:00; she may have been checking monkeys or other predators out of our sight.

The second female continued to go on for the night at regular hours, except one rainy eve with *Callicebus personatus* in the area (day 23, after 18:20). The first female, however, started to get in late from day 12 on, rain or shine, and by days 23 and 24 was coming in at 18:28 and 18:22 after long “dinner” sessions away, either eating or watching predators. On day 23, she had spent 36 min frozen on a perch near the nest at 13:00 before taking the food in her beak to the nestling, 16 min at the next visit, and 12 at the following. After a rapid visit, she again remained 11 min frozen

before feeding. We suspect that a hawk, maybe the *Buteo magnirostris* that started moving in along this road in the summer drought of 1994–1995, may have caused this freezing behavior.

At nest-1, brooding visits were short on day 6 and six rapid visits, between 13:00 and 14:10h, were without brooding. Starting on day 14, a hot day, there was no more daytime brooding. N. Formigone reported some brooding on brief watches on days 13–14 at nest-2; there was none on day 15 or (Oniki, Willis) day 17. On day 10, late rains caused the female to brood a lot, but rains kept her away from the nest for long periods on days 21, 23 and 24, with only rare brief feeding visits.

Brooding sessions, even on day 0, had medians of less than the 27 min during incubation. Medians declined 21-17-17.5-18-12-?-12-10-10-7 min on days 0–9 at nest-1. Other than the 88-min session on the morning of hatching, the longest sessions lasted from 30 to 33 min, decreasing to 20 min by day 11, and 15 by day 13. Short sessions watching the young started on day 12 and took over by day 14. The longest sessions of watching lasted about 15 min from then on, except for four long sessions (36–35 min on days 15 and 25, 48–46 on days 21 and 24). The first 1-min short visit was on day 3, with a few per day from then to day 12; on day 13 forward, most visits were of this type.

At nest-2, 3-day medians for brooding (one day of observation lacking in each triad) were 16.5, 27.5, 11 and 3 min to day 11. The longest sessions lasted 47 min on day 0, 30 on day 6, and 29 on day 10. One 1-min visit on day 0 presaged a few per day starting on day 6 on, and many brief visits from day 17 (or earlier). Sessions watching the young, on day 15 or later, were 2–12 min long, except one of 37 min on day 22.

On the 36-min watching session, the female lay down beside the preening young on a very hot afternoon (28°C), with sun on

TABLE 1. Food of nestling Cinnamon-vented Pihos.

Food	Age in days																											
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
No food	4/5 ^a	0/1				/1																						
Small ^b	9/12	19/17	15	6/5	6	/1	3/5	3	1/6	6/2	1/6	1	1/0	1/0	4/0	7/0	6	2/12	2/8	4/8	0/2	2/3	3/8	4/20	5/18	1/15	/11	
Insect ^c			2/0	2		6/6	6	4/2	2/2	1/2	2	0/1	1/1	2/1	5/0	2	1/0	5/1	2/1	3/0	0/1	0/2	5/3	1/2	0/4	/1		
Hopper	1/0		2/0		1/0								1/0									1/2		1/0				
Katydid ^d	0/1	0/2	5	5/1	8		8/0	9	4/1	6/0	3/1	4	4/0	2/1	5/0	2/0	2	1/1	5/1	5/4	2/0	2/2	10/1	3/2	7/3	3/2		
Beetle	0/1		2/0	1		1/0							1/0		1/0					2/0	0/1	0/1		0/1				
Roach				3				1		2/0		2/0	1/0						1/0			1/0		1/0		1/0		
Dragonfly				1		1/0		1/0				2							1/0				0/1					
Moth						1/0					1		1/0	1/0								2/0				1/0		
Caterpillar						1/0		2/0				3/0		1/0	1	0/2		2/0	1/0	0/1	2/0		1/0	0/1				
Spider								1		1/0		1/0							1/0	1/0	1/1		1/1					
Mantis									1/0		1/0		1/0					2/0	1/0	2/0		1/0	2/0	1/0				
Stick ins.												1/0						1/0	1/0		1/0							
Cricket												1/0		1/0				1/0				1/0						
Cicada												4/0	2/0	1/0		0/2	0/1	2/1	3/1	3/0		6/1	1/4	0/1				
Fruit												4/0	3/0	2/1				3/2	2/1	3/0	4/0	3/0	6/0	6/4	2/10			
% Fruit ^e												19	16	14	0	0	15	8	15	18	8	11	14	30				

^aNest-1/Nest-2; ^bHidden in beak; ^c1B (one beak long) or more; ^dGreen in 77 cases, orange in 12, dull in 41 (some may have been roaches); ^eMinimum (some “small” items may have been fruit).

TABLE 2. Feedings per hour watched on different days.

Day	Nest-1	n/h	Nest-2	n/h
0	10 + 3 ^c	0.90	14 + 4	1.28
1	19	2.06	19 + 1	1.53
2	19	1.69		
3	17 + 1	1.52	6	1.39 ^a
4	23	1.97		
5			(1) + 1	(0.89)
6	23	2.09	11	2.41 ^b
7	20	1.73		
8	12	1.75	9	1.44 ^a
9	19	2.18	4	1.23 ^b
10	7	1.62	9	1.79 ^b
11	10	1.79		
12	12	1.95		
13	20 + 1	2.37	(2)	(4.26)
14	19	2.20	(1)	(1.30)
15	20	2.15	(3)	(2.4)
16	11 + 1	2.12		
17	4	2.70	17	1.59
18	21	1.85	15	2.63 ^b
19	22	1.89	15	2.54 ^b
20	19 + 1	1.57	5	1.98 ^b
21	13	1.33	9	1.49 ^b
22	24	1.97	14	2.05 ^a
23	26 + 1	2.10	27	2.28
24	25	2.09	34	2.92
25	7	2.37	34	3.57
26			12	2.55 ^a

^aMorning; ^bAfternoon; ^cOn without feeding.

the young bird; she left to chase another piha. The young soon stopped preening and settled, as usual whenever the female left. For the 48-min session, a warm midafternoon

after morning showers, the female stayed upright next to the preening or even wing-flapping young; it once gaped at her but resumed preening when she didn't leave. She froze watching to her left (west) for some time, and the young stopped moving until she started turning her head again. The bill-up young gradually sank down flat on the nest. The 46 and 35-min sessions were in the morning, but with sun on the young. Both mother and young froze for about 20 min between preening sessions in the first case; in the second, the upright female pecked the young rump twice but it just preened more; after three feedings in a row an hour later, it flew from the nest.

The 37-min session at nest-2, on a cloudy midmorning after a rainy night, the young preened busily except for a 5-min freeze, as the upright female looked about just behind the nest. This female spent much less time and fewer sessions watching the nestling than did female 1, as noted above. Her main afternoon of watching was on day 17, when two male howler monkeys were around and jumping on small trees, and on day 23 with rains.

Both females left the nest early, as during incubation, when almost too dark to see them; the owls had barely stopped calling, and the first crepuscular birds (forest-falcons, *Grallaria varia* and *Chamaeza* spp.) were just tuning up. The first female left between 05:24 and 05:33 (mean of 5 records, 05:29 h), the second at 05:36 and 05:38. There were often several feedings of young, at times one after another in the near-dark before 06:00 h, at least from day 9 on, in contrast to lack of feeding in the evening.

After-hatching nest-approach. As during the incubation period, the female often approached the nest cautiously, with several stops to look about, frozen or with a sudden "bow and scrape" of 90° or a "reverse" of 180°. Later visits during the nesting period often seemed

TABLE 3. Feedings at different hours of the day.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Nest-1	12	21	26+1 ^a	43	28+1 ^a	37	38+1	38	34	35	37	38	28+3	7+3
Per hour	(2.7)	1.75	1.54	2.46	1.51	1.94	1.86	1.91	1.73	1.74	1.84	1.88	1.73	(3.15)
Nest-2	7	15	19+1	20	18+1	19	13+1	22	27+1	28+1	26	21+1	23	1+2
Per hour	(5.5)	2.44	1.99	2.0	1.76	1.69	1.43	2.08	2.47	2.65	2.17	1.90	2.71	(2.63)

^aOn without feeding.

rapid, although we often failed to detect her until she flew to the nest tree at any time, since she could fly several m from one perch to the next in a blink of the eyes. At nest-1, other than the extreme series noted above, there was a case of her freezing enroute for 28 min, on her last visit of the day on day 18. She froze 19 min on her “favorite” approach perch (an open horizontal vine below and behind the nest tree), skipped her perch “C” low in the nest tree and went directly to perch “B” for 9 min, then up to perch “A” next to the nest and reached the nest at 18:02, more or less a normal hour for this female. She often used this sequence of perches on the approach. On day 21, she took 15 min to get to the nest, again with food in her bill. Here she went favorite-behind trunk-C-B and stopped for 14 min, the mantis in her beak eventually almost escaping; finally she went to A and the nest.

On day 3, she took 10, 5 and 4 min on successive approaches because of passing marmosets. She was on the nest for 20 min after the 10-min approach, then left and, after a pause, attacked them several times. The adult marmoset ducked its head and descended its vine with each attack. It watched her intently after each attack, climbing trunks under 10 m from the nest and peering about, while young marmosets played; the piha finally preened and flew off nearby for 14 min. The marmosets moved off, perhaps disturbed by Oniki, but were

around the next day. They were attacked by the piha above the road at 06:17 (Willis scared them off by approaching). On day 2, the female had frozen 9 min on a perch 20 m from the nest, green katydid in her bill, looking upward, before flying to C-B-A. A large dark bird, probably a hawk, flew through the upper midlevels 18 min later; a band of *Cebus apella* was approaching, and perhaps *Harpagus diodon* was following them. She waited 2 min on her favorite perch on the next approach, 25 min later.

Not counting the above cases of 9 or more min on the approach, nor the many approaches of less than 0.5 min, we recorded 144, 56, 26, 11, 10, 3, 2 and 0 approaches of 1 to 8 min in duration, respectively. Repeated approaches of 2–3 min on day 0 and of 2–7 min the whole afternoon of day 6 suggested unknown problems.

The female at nest-2 stopped less on approach, or did so on perches not visible from our observation point (the nest was uphill and not so close as nest-1). One 9-min freeze near the nest, with a big green mantis in the beak, was observed on the afternoon of day 21. Records of 42, 16, 3, 2 and 3 approaches of 1 to 5 min in duration, respectively, surely underestimate total approach time; the female was only seen as she arrived, mostly on the limb just behind the nest, on many occasions.

Feeding. The female hid small or large prey

TABLE 4. Fecal sacs during nest life.

Day	Nest-1		Nest-2		Per hour	
	Eat	Off	Eat	Off	Nest-1	Nest-2
0	1		2		0.1	0.2
1	4		3		0.4	0.24
2	8				0.7	
3	10		1		0.9	0.23 ^e
4	12				1.0	
5						
6	13		4		1.2	0.9 ^d
7	11				1.0	
8	9		3		1.3 ^d	0.5 ^e
9	7		3		0.8 ^d	0.9 ^d
10	4		3		0.9 ^d	0.6 ^d
11	5				0.9 ^e	
12	8	1			1.5 ^d	
13	9				1.1	
14	5	2			0.8	
15	4	2			0.6	
16	2	3			1.0	
17		1	9		0.7	0.8
18	5	2	8		0.6	1.4 ^d
19	3 ^a	4	7		0.6	1.2 ^d
20	2 ^a	5	2		0.6	0.8 ^d
21	2	2	5		0.4	0.8 ^d
22	2	6	7		0.7	1.0 ^e
23	2 ^a	6	9 ^b	1	0.6	0.8
24	5	4	10 ^c	1	0.8	0.9
25	1	1	8		0.7	0.8

^aOne fell; ^bTwo fell; ^cThree fell; ^dAfternoons; ^eMornings.

inside the beak, sometimes with wings and antennae projecting. Large katydids (including green-leaf mimics), cicadas, mantises, stick insects up to 10 cm long, roaches and beetle-

like insects were common, moths and caterpillars less so; small unidentified insects completely hidden in the beak were detected only when extruded at the gape of the young (Table 1). Fruits of many different colors and shapes, including palm fruits, were brought from day 13 (nest-1) and 15 (nest-2, N. Formigone observ.) on, especially the last few days in the nest, but this cannot be considered a frugivorous species in feeding young. Four cases of the bird bringing 2 medium fruits at a time and one of 3 fruits suggest that the nutritional value of fruits may be low, hardly worth a return to the nest unless several are brought or the fruit is very large. Big and round fruits may be hard and difficult for a young bird to swallow, unlike long insects, restricting fruit use further.

We suspect that fruits may be brought at the rapid visits before 06:00 h (4 on day 26 at nest-2, perhaps 6 on days 15 and 17 at nest-1), at least late in nest life, for it is hard to believe the female could get insects rapidly in the semi-dark. In some cases, however, the piha brought a big insect before 06:00 h, not the tiny items usual at that hour. On day 25, the second piha brought 10 fruits even during the daytime (plus 9 insects and 15 medium or small items hidden in the beak; the last were likely mostly insects, for a small fruit would be of little value). The first piha brought 8 fruits on days 24 and 25, plus 18 insects and 6 tiny items, on daytime visits; she was below Oniki and closer at this nest, and identifying prey easy as she passed it to the young at the last moment.

Long mantises and stick insects projected from the female's beak and, being alive like most prey, sometimes walked out of her beak or that of the young. The female had to chew and beat them on approach perches, even dive after ones that fell from the nest. The huge beak of the young, which lifted and opened suddenly only about 10–30 sec after the female came to the nest edge, managed to

TABLE 5. Fecal sacs at different hours of the day.

	Sacs at given hour													
	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Nest-1	3	7	8	13	9	14	19	17	9	18	15	22	17	3
Per hour	0.7	0.6	0.5	0.7	0.5	0.7	0.9	0.9	0.5	0.9	0.75	1.1	1.0	(1.4)
Nest-2	0	3	6	5	4	4	6	9	10	13	10	9	8	
Per hour	0	0.5	0.6	0.5	0.4	0.4	0.7	0.9	0.9	1.2	0.8	0.8	0.9	

engulf prey that looked far too large. However, cicadas seemed to be different, with the projecting eyes catching if the female had not removed the head first. Table 1 shows that cicadas only were brought from day 13 at nest-1 and day 17 at nest-2, the same time as fruits started. One large cicada fell from the gape of the young and was lost on the ground, despite a dive by the female. All items were inserted head first.

Except for large items, feedings were instantaneous, food disappearing into the closing beak as if into a flap-top garbage can. Since the young never stood or made any move other than beak-up, it was as if food vanished into a dark leaf. No sound was ever noted.

Feedings per hour were few the first day, then 1.5–2 per hour, rising to 2–2.5 per hour the last two weeks in the nest (Table 2). Both birds fed young rapidly the day of nest departure and a few days before. Marmoset problems dropped the tally slightly on day 3 at nest-1; clouds and rains on days 7–8 and 10–11 caused slight drops. Rain slowed feedings to 1.3 per hour on day 21 at nest-1 (Table 2); the day before, an absence from 06:00 to 08:30 h for unknown reasons caused a low tally. Hot, dry weather on days 18–19 may have caused another drop at this nest near the forest edge.

At nest-2, rates were slower the first two weeks and faster the last two, compared to

nest-1. Clouds broke the early heat wave a bit on day 6, perhaps allowing faster feeding that afternoon; but some rain the afternoons of days 9–10 may have slowed feedings. Rain slowed feedings slightly the afternoon of day 24, and late the preceding afternoon (or *Calli- cebus* monkeys? the female went on the nest very late, see above), but rapid feeding the morning of day 24 made up for both. However, monkeys nearby may have caused slow feeding late on day 17.

Feedings were rapid on pre-07:00 h observations at both nests, with another peak between 08:00 and 09:00 at nest-1 (caused mainly by rapid feedings on days 13 and 23 when, for unknown reasons, the feedings were slow from 06:00 to 08:00, due to 50 and 31, plus 58-min breaks; perhaps those were predator problems, for the female froze 2 min on approaches). Rates were fairly high during the rest of the day (Table 3), after a 09:00 (or 09:00–11:00 at nest-2) break.

The first day and on the last visit of the day, the female sometimes returned and brooded the young without feeding. In one midday case, she swallowed her food and attacked a *Chiroxiphia caudata* on seeing it 2 m from the nest.

Fecal sacs. The female often had to dive across for a fecal sac, signalled by some lateral twitches of the young bird's small tail, but she either ate the sac instantly or (female 1) car-

ried it off in the bill. At times, she dove after a sac that fell, catching it in the air and eating it or carrying it off. When she missed, as occasionally late in nesting, the sac went to the ground. The second female even dove once for a dropping sac after the young left the nest.

On day 0, fecal sacs were eaten at 14:07 at nest-1, and 15:04 and 17:35 at nest-2, some 8–9 h after hatching. One of the latter two may have been the remains of the large katydid fed at 08:32. Sacs were earlier on following days, at 11:24 on day 1 and 10:11 on day 2 at nest-1, 13:30 on day 1 and 11:18 on day 3 at nest-2 (dawn feedings not observed), indicating more rapid digestion. Thereafter, small sacs were recorded from 07:00 h on, not counting single large sacs regular at dawn or between 06:00 and 07:00 h that must have been from food eaten the day before. Further sacs reappeared from 11:00 h on the first week, 09:00 on the second week, and between 08:00 and 09:00 h on the third and fourth weeks, at least at nest-1 where observations were easier. At nest-2, sacs seemed smaller, the female eating all of them, even when having to catch one as it fell. Number of sacs rose during the first few days and thereafter was about 1 per hour of observation (Table 4), decreasing somewhat as larger sacs were produced later during the nesting life at nest-1 (perhaps slightly so at nest-2). More sacs were produced per hour from 11:00 on, with a peak at nest-1 after 17:00 (at midafternoon for nest-2; Table 5). Removing observations on the first two days at each nest, when production of sacs was low, raises rates slightly at nest-2, especially at 06:00 h (0.75 per hour) and 07:00 (0.8). At nest-1, there is little change.

At nest-1, the female began to quickly carry some large (rarely small) sacs away from day 12 at 13:15 h on, for she had been stopping brooding after feedings. The sacs were dropped from perches 5–15 m off in most

cases, and seemed very sticky. The female often had to shake the sac free, wipe it off on the perch, or wipe her bill after dropping it. She could shake her head afterward. Once she finally ate a sticky sac that she had carried off.

After-hatching nest departures. Intervals off nest-1 ranged from 2 to over 138 min, with a median of 19 min (8 min shorter than for incubation, but almost equal the 18-min intervals for the incubating female at nest-2) in 405 cases. There was a wide flat peak between 4 and 20 min (197 records) off the nest, tailing off past 40 min (135 more records); 108, 103, 91, 87 and 82 were long records. The record of 108 was before dark the day before the young left, and the female had been busily feeding the young and repeatedly watching it preen all day; she may have needed to forage for herself. The record of 103 on day 19 was preceded and followed by bouts of feeding; later that day there were intervals of 91 and 66 min. There may have been predator problems, which could have been the case also for the record of 108. Day 19 was also very hot, 31° at 13:22, but the female fed 5 times between 12:00 and 13:00 and took off 91 min thereafter. The record of 87 min was linked with a 53-min break, on day 15, between 10:00 and 12:00, perhaps due to a predator in the area. The record of 82 min, on day 7 near 09:00–10:00, was followed by longish intervals of 47, 15, 48 and 39 min between 12:00 and 15:00, then by a lot of brooding on a foggy late day.

Intervals off nest-2 were similar, ranging from 1 to 92 min with a median of 17 min (much as during incubation) for 246 cases. As for female 1, there was a wide flat peak or “mesa” between 4 and 19 min (130 records), but with a lower side “mesa” of 27 to 33 min that had been only moderately noticeable for the other female; we noted a slight tendency for female 2 to alternate long and short trips. An absence of 76 min was due to the two

Alouatta fusca nearby on day 17, with a linked absence of 57 min just after. One absence of 85 min took place when a band of *Cebus apella* passed just before the female called the young out of the nest. The record of 92 min late on day 9 had been preceded by records of 55 and 6; it was a bit rainy, but the female brooded the young much less than she did on the rainy next afternoon, so we suspect predator problems rather than rain. Later, on day 25 when the well-feathered young was left partly on its own for a rainy afternoon, there were intervals of 73 and 63 min, plus seven of 30–40 min, as well as four of 5–9 min.

Leaving the nest, the female often stopped to look about 5–10 m off, then flew on or started foraging. She often flew out of sight. When not, she busily sallied for insects, visited melastome and other small trees for fruit, or preened up to 10 min. Occasionally, a female descended to 2 m up to peer about in the understory. She could regurgitate or defecate seeds, indicating that she was frugivorous even when the nestling was not. The regurgitated seed makes a noise when it hits the leaf litter, whether the bird is on or off the nest. She regularly ate small insects as well, once a katydid.

Three times, after 1, 9 and 13 min brooding, female 2 attacked a male (noisy) piha or silent piha up to 20 m off. The first female attacked a passing piha once. Once each, the females attacked *Chiroxiphia caudata* near the nest. The first female attacked a *Sittasomus griseicapillus* climbing near the nest, but ignored them in general. Out foraging, in a fruit tree over the road, female 2 twice attacked a noisy male. Pihas in molt passed the nest or even sang nearby (once) with no problem if the female was away. Once female 2 supplanted a *Myiodynastes maculatus* that foraged in the melastome behind her nest for several days. Once she supplanted a passing *Attila rufus*. She did not join mixed flocks, but sometimes wandered near them as they

passed or kept an eye on them from the nest or other place. Falling leaves could be watched as the female brooded or waited; a scraping limb startled female 1 once.

Departures at nest-1 were often S toward the road, in contrast to during the incubation period. Perhaps the female had been avoiding Melo and Antunes, who watched from the road close to the nest because the female didn't seem bothered (Oniki watched from the far side of the road, often from the car, except when filming, to avoid being very close). The female went W or NW on 38 departures, N for 40, NE for 19, E or SE for 39, S or SW for 45. Several abrupt 90° or even 180° turns were recorded after she stopped, and return directions were often different from departures, as during the incubation period.

At nest-2, right-angle or returning departure movements were also noted, as during incubation. Returns were often from a different direction, too. Easterly headings off the nest were much more common than during incubation, despite the tree trunk, perhaps because the female often started from a standing position, or because new fruiting trees were off east. She went W or NW on 51 departures, N or NE on 24, E or SE on 73, S or SW on 33.

Young. The nestling was flat and fuzzy on the nest, seeming a hairy caterpillar or leaf, most of the day. The down was pale orange and rather conspicuous in any sun-fleck, probably a mimic of hairy and urticating caterpillars (a somewhat similar strange young bird is shown for *Laniisoma elegans* in Snow 1982). The beak was already dark above on day 1, with no sign of a pale gape angle at all. The lower mandible is pale at the base underneath. Opening the yellow gape to feed, and twitches of the rear end to defecate, were the only movements noted; even hovering mosquitoes alighting on the forehead caused not

a move. A deerfly walking ahead did cause a slight twitch on day 2. The whole aspect is of a sick or almost dead slug or larva.

During the last 13 days, the nestling developed feathers slightly paler and buffier than those of the female. It started to preen actively when the female stayed watching, and eventually even preened briefly at times when the female was away. It became so large that it appeared a bird sitting in the foliage, with no nest below, even looking like a short-tailed dull buffy-gray female out of the nest, or like one of the pendent gray dead *Cecropia* leaves about. By day 6, the eyes were open. In general, the eyes opened only briefly or when the female was present, except the last two or three days. The head can be up a bit, at least from day 8 on, for a short time after the female leaves.

Even early, the young must have occasionally moved or opened its beak under the female, which half-stood and looked under her, or shifted on the nest at times. She no longer made trampling movements, which probably turned the egg during incubation, but she turned or shifted at times; she was rather high and fluffed on day 0 until she got used to the young. On day 11, the young stuck its head out from under her, opened its beak briefly, and she left as at a green light. By day 12, the young could point the beak up with eyes closed for a minute or two, with bill champing, as the female left; it preened briefly once.

Yawning was noted on day 13, also opening the beak for short periods when the sun hit. Tail-twitches were noted on day 15 and earlier, even tail up and twitched at times as the young rested with eyes closed and head down with no female near. It gave a double-wing stretch on day 15 to end preening, when the female left. By day 16 it was large enough to lean on the trunk next to the nest to rest. On day 18, both young were flapping their wings at times, falling down, and resumed

preening next to the female; later nestling 1 pecked at the nest material during preening. This young, beating wings on day 19, raised a lot of dust (from the nearby road?). Noise from *Pyrrhura frontalis* caused nestling 2 to crouch low on day 19. It was again low and quiet for several hours as howler monkeys sang on the afternoon of day 20. Even on day 20, a mosquito that bit its forehead did not cause the first young to move when resting. On day 21, the young flapped so hard it almost flew. On day 23, the female poked the young with her bill, seemingly to get it to preen. The second young, on days 23 and 24, was so itchy it often preened busily even when the female was not there. On the latter afternoon, it had to beat its wings to shake off rain, as the female did not return. Later the young just sat low as it drizzled. Early on day 24, the young turned back and forth actively while standing to preen, or beat its wings a few times; it champed the beak on two occasions to scare different mosquitoes that alighted on it when the female was gone. The pale areas about the eye were featherless, the wings darker than the body. The female had to stand outside the nest as the young preened, or move aside for its movements.

Nest leaving. Just after the female fed at 08:32 on day 25, the first young flew to a nearby vine, then off N downhill out of sight. The female waited 10 s, then flew after it.

At 10:17 on day 26 at nest-2, shortly after a band of *Cebus apella* passed, the female fed and flew 2 m S, starting a strange downscale sound like several rapid puffs of air, “uf-uf-uf-uf-uf-uf-uf,” the only vocalization heard from her (wing-whirrs were noted in an attack on a large woodcreeper, see above). The sound can be imitated if one whispers it rapidly.

The young preened, hopped on the nest with a try at fluttering, then turned its back to the female and sat down. The latter repeated the puffing several times, and it finally turned

back, gave two quick flights up toward her, ending on a swinging vine in the open 1 m above the nest and 0.5 m SW.

The female came at 10:24 and fed it. With some fast-puffing notes, she led it upward and SW to near Willis, then turning NW and up into the subcanopy some 22 m up and 20 m NW of the nest, by 10:45; she fed it 3 times on the way. At 11:16, she fed it after it preened a bit; she gave the puffing notes off E but stopped. At 11:24, she brought an insect, then called the young north on several flights, ending 23 m up on a small horizontal twig. On one flight, it almost fell from the perch, but recovered; the last flight was 10 or 15 m. Before it flew, it did a full stretch on one side and defecated a seed. At 11:50, the female fed a green katydid, at 11:54 something small, 12:01 again (with one puffing series), also 12:48, 12:50, and 13:09 (with a dive after the dropping fecal sac, which she caught and ate). At 13:12, she fed, then waited 30 cm from the young until 13:28 as the young preened busily. Her visits were now direct, with only one stop to look around before going to the young. The young stopped preening when the female left.

Nest destruction. The first nest was nearly gone a few days after the young left. Skutch (1969) recorded the Rufous Piha (*Lipaugus unirufus*) with fledgling destroying an abandoned nest, perhaps to avoid giving predators a “search image” of that type of nest.

DISCUSSION

Our study indicated that *Lipaugus lanioides* is very similar in food to such forest-edge tyrannids as *Myiodynastes* sp. and relatives. Young are fed insects, adults feed on both insects and fruits captured with short sallies or by sidling up and pecking. Short legs and limited ability to hop about, large wings and big gapes (even if bills converge on thrush beaks)

are all very tyrannid. We would not be surprised if pihas (and perhaps other cotingines) arose as a side branch from some regular tyrannid stock, perhaps even close to the similar *Rhytipterna* species as an offshoot of the *Myiarchus* group (Lanyon 1978). However, nests are unlike myiarchines, being thin twig structures like *Empidonomus* sp. and outside of cavities.

The question then is, why do piha males not help raise young, as in forest-edge tyrannids with similar fruit-insect use? Male tyrannids rarely help incubate, but often guard their females and keep strict territories that exclude philandering males or provide food supplies (Willis 1995, Skutch 1960, and others). We suspect that female-only nest care evolved in the piha lineage as they entered the forest midlevels, specializing on large fruits and insects. Increased fruit use, dark midlevels, different predators, and other changes could have caused modifications in the pihas, for instance their inconspicuous behaviors and colors (gray, rufous, etc. in the various species). Later other lines with bright-colored males, such as bellbirds, could have evolved from such lines as the pihas.

Obviously, our detailed study of piha nesting can only start to answer questions about them and about female-only nesting. Before discussing hypotheses (frugivore non-territoriality, poor visibility, predators), we would like to comment on four earlier ideas: that fruit eating leaves males free to philander (Snow 1963), that females wandering after fruits cause males to waylay them at “hotspots” (Bradbury 1981); that female fruit eaters go for a few males with good genes, “hotshots” (Beehler & Foster 1988); and that females avoid or attack competing males (Willis *et al.* 1978).

Philandry in fruit eaters. As fruits are abundant and easy to locate, females can raise young unaided by males which, “emancipated,” can

turn to well-nourished philandry (Snow 1963). Piha males could well use fruit to have free time to call for females, an aspect we did not study. The female pihás were eating some fruits themselves, which aided them to get food, even if they fed insects to the young birds. Older young do receive fruits. However, the female could have raised more than twice the number of young if the male had helped, for he would not have to spend time brooding or watching. Wolf *et al.* (1988) showed that 2.6 times as many young were produced when the male was allowed to help in juncos.

Snow & Snow (1979) suggested that the small nests of manakins and pihás limit the number of young. Willis & Oniki (1979) noted that nests are large in other nonmonogamous tyrannids that eat insects or insects and fruit, but Snow & Snow (1979) made an important point: small size of nest, to avoid detection by predators, could limit brood size and make male help superfluous. However, the male could feed young and they could leave more rapidly, even from a small nest, if growth rates are not limiting. Male *Todopleura*, even though quite frugivorous, help feed the single young at forest edges (Willis & Oniki 1988). We discuss these arguments below, under "predation".

Hotspots. Frugivorous males and females do wander (Lill 1976, Bradbury 1981), for fruit locations change seasonally. In a nonmonogamous population, female movement probably allows a male to encounter several females and vice versa. Movement of females also makes male territorial behavior difficult, for fruit distribution changes much faster than insect distribution (see below). However, female territoriality is known in nonmonogamous female woodcreepers (Willis 1972), and female manakins with radiotransmitters seem to have nonoverlapping areas of use (Foster 1996). Certainly, the female pihás occasionally

attacked passing males near the nests, and one male in São Paulo was singing next to a fruiting tree that could have attracted females. We did not study this aspect in detail, but doves, parrots and tanagers are monogamous frugivores, and males easily follow their mates, as do some monogamous birds of paradise. Below, we suggest that predation and poor visibility could be the reasons why forest-interior frugivore males cannot follow and guard their wandering females from EPC's. In a review of the literature, Møller & Birkhead (1995) found less male help with young if EPC's occurred, although not in all species.

Hotshots. We did not specifically study whether older male pihás with much experience ("survivors" with "good genes") get more copulations, or if satellite males lurk near them waiting for females to approach (Beehler & Foster 1988). Piha males seem to sing occasionally at various places, even near the nests we studied at times; but there is a group of singing males at one place between the two nests in Nova Lombardia and isolated males sing regularly at certain other sites there and in the reserve of Santa Lucia. Given that pihás are nonmonogamous, it is likely an advantage to a female to select the best male in a large area. If female tyrannids engage in EPC's with distant males with good genes, as do many females of nonforest birds, the female could gain this advantage without losing the help of her mate. However, her mate should guard her, a difficult thing to do in forests and other places where female-only nesting has evolved (see below).

Competing males. A male could eat food needed by a female and her young, our earlier hypothesis for female-only nesting in insectivorous woodcreepers, where direct competition with males occurs over small ant swarms that flush prey (Willis 1972, 1979, Willis *et al.* 1978). The female pihás certainly attacked noisy males

and silent pihas near their nests, suggesting that these birds (and others attacked, notably fruit-eating *Chiroxiphia caudata* and *Myiodynastes maculatus*) compete near nests or could attract predators. Female-only nesting in insectivorous *Myiobius* sp. that fly about under mixed flocks could result from lack of prey with the extra bird present. However, we recently suggested that males are not avoided because of food competition, but because of attracted predators in the nonmonogamous *Dendrocincla* woodcreepers (Willis & Oniki 1995). The monogamous male could help feed young, and unhelpful males wander in anyway even in nonmonogamous birds, as the pihas. The nonterritorial or female territorial systems of nonmonogamous species protect only a small area around the nest, part of an ant swarm or bird flock or against females, and do not keep male competitors out. We doubt that the female piha, so very silent, could defend much beyond the limited range of her vision in a dense or dark forest understory.

Territoriality. Related to Lill's (1976) hypothesis of female movement, one of the main ways males guard mates, via territoriality, is difficult for male frugivores. Fruit distributions change rapidly, as do flower distributions for similarly nonterritorial or locally territorial hummingbirds. Hummingbird "territories" are often small patches of flowers, which can hardly stop females from moving out from or males from moving in on a possible monogamous bond. Even nesting territories do not stop EPC's in some species, though we think (Willis 1995) that long-term tropical territories are likely to be more effective than the "Wild West" of temperate-zone short-term territories in stopping fence-jumping by "hotshot" males and "nobelistic" or "eugenic" (gene-chasing) females. Additionally, defending territories in cluttered and dark sites like the forest interior may be dan-

gerous (see below).

Colonial males partly avoid this problem by guarding females when nesting jointly, though wandering to feed even more than do frugivores; but they have more problems with EPC's and with alien eggs in their nests. Other problems with territoriality for pihas and forest birds are noted below.

Female guarding. Guarding females, as do monogamous parrots and tanagers, is a well-known alternative to territoriality (to prevent EPC's) even for frugivores. Male tyrannids of forest edges do guard their females during fertile periods (Willis, observations of *Capsiempis flaveola*; Skutch 1960). Below, we argue that guarding females is dangerous in dark forests, dense prairies and other habitats where many nonmonogamous species occur. We cannot suggest any other advantage of lack of female guarding in certain tyrannids and not others.

Predation. Snow & Snow (1979) suggested that predation on nests could be higher if activity at a nest is greater, favoring small clutch size where a female can work alone. Wrangham (1980) suggested that males trying to copulate with females near nests could attract predators. We have suggested that predation on adults leads to females avoiding males in the forest (Willis & Oniki 1995). Judging by the dozens of apparently antipredator behaviors and morphological patterns we detected in our study of piha nests, we now think predation of adults or nests are likely reasons for evolution of nonmonogamy in pihas.

We have never, in fact, seen such an impressively antipredatorial bird as the piha, except perhaps the similarly dull and sneaky *Dendrocincla* woodcreepers. Dull colors, slow movements except for fast flights at unpredictable intervals, almost silent, it is remarkably hard to detect except for occasional loud calls of a male. The egg is protectively col-

ored, like many tyrannids. The young bird is protectively colored, dull like a fallen leaf, but with orange fuzz imitating a hairy caterpillar until it gets a buffy gray plumage that blends well, for instance with dead *Cecropia* leaves pendent here and there at the same forest levels.

The nest is a mere thin platform, almost invisible when the bird sits on it, rather seeming a bird perching normally. Construction, however, takes many days, with scattered visits and careful approaches, with stops to look around for long periods, sudden flights, etc. In particular, there is no worried male guarding the fertile female, which could attract attention of predators that could remember a nest location or attack the adults. In monogamous forest antbirds and ovenbirds, near the ground or in dense foliage, the male helps build, and does not guard the female, while the nest may be in a cavity or enclosed. Monogamous female-guarding species in the forest either nest in cavities (parrots) or live in the open canopy or edge (most parrots, tanagers, doves) where predators can be seen from afar. One should remember that, physically, the canopy is just another forest edge if one pretends that the forest interior is flooded to 20 to 45 m up, as in Amazonia when the rivers rise (Oniki 1985).

What happens to cause this difference in female guarding between the forest-canopy frugivores and the forest-interior ones? We think the difference is partly one of two well-known types of predator attack, recorded even in reptiles and fish. In the canopy and open, hawks and falcons hunt by fast flight, for they can see and be seen far off. In the forest interior, sit-and-wait hawks and owls attack from hiding, for fast raptors cannot see their prey far off, nor fly fast, while the prey cannot see a waiting raptor very far off. Entry of tyrannids of forest edges into the forest must have caused a sudden change of hawk attacks, from the active to the passive preda-

tor styles. Movement of birds inside the forest would be linked with attack by sit-and-wait predators, perhaps explaining Beehler's (1985) observations of nonmonogamy mostly in "traplining" birds of paradise.

In the edge or canopy, where most tyrannids live, a male following the female can see the distant hawk better, and give the alarm in time to help the female escape. In the forest, the attack is likely to be sudden, at short range, and both male and female run a risk because the moving pair are doubly visible while the waiting hawk or owl is not. Antbirds and ovenbirds that forage near the ground, a cavity, or a bit of dense foliage on a trunk are safer, as they can hide with a quick movement. Pihas wander in the open midlevels, as do most forest-interior flycatchers, in part because tyrannids are specialists in sallying long distances for food, while antbirds sally short distances and ovenbirds do not sally, just peck nearby trunks or foliage (This results in periodic long-distance moves between foraging perches for tyrannids, gradual movement by others). *Dendrocincla* woodcreepers, nonmonogamous, also live and fly in the open forest midlevels (Willis & Oniki 1995). In a sense, all these nonmonogamous birds are "trapliners", because they often move to a distant perch (at some 2 times the normal foraging distance), and can check for predators only as they arrive. The male cannot help much, as he has to keep out of the "foraging circle" of the female, and vice versa.

Fruit eating in the forest does not necessarily lead to nonmonogamy. *Triclaria malachitacea*, a sneaky monogamous forest-interior parrot, is one of the hardest birds to see in Nova Lombardia, while pairs fly and forage together, mostly without "traplining".

Following and guarding females are also difficult because of the dark environment, trunks and foliage, and sudden, evasive moves of the female, as we noted when trying to follow her to see where she was foraging. How-

ever, this is not a problem of vegetation but of predation. The female is perfectly able to detect the male a kilometer away by his call, and he could also detect her call at great distances, as in ant-following antbirds (Willis 1967, 1972b), if it were not so dangerous for her to call as she moves about. The calling male piha stays in one or a few places, watches long periods to be sure no hawk or owl is about. Moving together is dangerous if birds call, except when they move in dense vegetation and can hide short distances away, as do antbirds near the ground or ovenbirds in dense foliage above the ground. Silence of the female piha is really remarkable, except the whispered puffing she has to use to lead the young bird about. Even when she attacks a huge bird, there is only a sudden whirr of wings, audible only at close range. Similar predator problems with following females occur in grouse (Tetraonidae), which are large and slow and very visible, even when they live in dense scrub, perhaps explaining nonmonogamy in the group. Johnsgard (1994) notes that large and bushy-area conspicuous grouse seem less monogamous than small understory (hidden) or open-zone (male helps watch) ones. Whitcomb *et al.* (1996) have recorded extreme loss of nesting females and nests even in a forest species of grouse.

Male tyrannids have to keep out of the rather large foraging circles of their females and vice versa, so the closed environment causes even more difficulty in mate guarding than for a male that can forage close to his mate, as in parrots, antbirds and other short-distance nonsallying birds. Also, a female tyrannid sits quietly between long-distance sallies rather than forage constantly, causing even more difficulty for a male that has to be sure she is not meeting another male. An intruding male can also sit quietly, making him hard for the guarding male to detect.

Territoriality, the other way males guard females, is also difficult for a forest-interior

sallying bird. To fight for a territory in the open forest midlevels, where a hawk or owl can wait behind any little foliage while the moving birds are visible and far from cover, is more dangerous than in denser foliage next to the ground (monogamous, territorial antbirds and a few tanagers) or upper-level dense foliage or vines (monogamous, territorial ovenbirds or canopy tanagers). We rather doubt that female pihahs have to move much to find katydids or fruits, as Lill and Bradbury suggested for frugivores. Nonmonogamous female omnivorous manakins certainly have their own small separate home areas and, perhaps territories (Foster, 1996). It is even possible that female pihahs have their own stable separate territories with only rare fights, as do female nonmonogamous dendrocinclahs (Willis 1972). The nesting females certainly attacked any piha that passed the nest, and yells from many attacked birds but never from the females suggested that most trespassing birds were males.

If a male cannot guard a nest-building and fertile female, she is almost certain to copulate with outside male "hotshots," causing mate desertion by the male. Also, each male becomes a "hotshot" wandering over the areas of several females (as in dendrocinclahs, Willis 1972) and moving in on each one as it nests, attracts fertile females to a fruit tree (the male piha at Barreiro Rico?) or calls them to him or a group of males in some good site for him and her both.

We noted that, at least at Nova Lombardia, the majority of mixed flock members are monogamous, and pihahs and other nonmonogamous birds are seldom members. Some small nonmonogamous birds that join flocks, however, are *Myiobius* spp., *Oxyruncus cristatus*, *Sittasomus griseicapillus* and *Dendrocincla turdina*; the middle two species do not sally much for prey. Large birds like pihahs may scare the small birds in mixed flocks and be unable to join because they look too much like an owl

or hawk in any sudden flight. Inability to join mixed flocks could force large birds to wander alone, where travel in mated pairs becomes conspicuous.

Monogamous toucans and toucanets, however, do wander in small or mixed-species groups, mostly in the canopy. *Selenidera maculirostris* is a forest-interior toucanet that differs from pihas mostly in not sallying and in nesting in cavities. This could indicate that nest predation is more important than adult predation for evolution of female-only nest care, though dendrocinclas are nonmonogamous despite protected nests. *S. maculirostris* in groups could help each other look for predators, though pairs would be less efficient or even dangerous. *S. maculirostris* also forage mostly in sprays of foliage without sallying, where they are safer and can work closer together than sallying pihas; they do move little for long periods.

The nesting female piha attacked various possible nest predators, such as marmosets, a hawk, and a large woodcreeper. The females could also stay long periods following and watching toucanets, monkeys of various species, and seemingly watching bird flocks near the nests. Long absences from the nest, sudden flights from it at a passing large bird, all indicate that the female is alert to danger in her exposed nest. Males help by guarding nests if mobbing predators is possible (Markman *et al.* 1995 and included references), but forest-interior nonmonogamists hide rather than mob, perhaps due to presence of sneaky predators that could catch adults and/or young, even at closed but large nests in the case of *Myiobius* sp., reducing the value of male help.

The single egg of pihas indicates a limit on brood production. The helpful male could attract more predators, as could the increased commotion with two young competing for food. Two young do fit in small nests of manakins and hummingbirds, without a great

deal of commotion, but these are much smaller birds.

It is unknown whether more food brought by a male could help the single piha or two manakin or hummingbird young leave the nest faster. For a bird nesting in a predator-rich environment, the piha incubates and feeds the nestling for many days. Skutch (1969) registered even longer periods in another piha. It is not clear if long periods are related to a thin nest, which could lower nest temperatures, or to some other factor. Tyrannidae in general, however, have longer incubation and nestling periods than do songbirds, and pihas could be unable to change this even in a predator-rich environment. Thus, it may be that even the extra food the male could bring would not speed up development. The young flew relatively well when it did leave the nest, a necessity in short-legged tyrannids, since young or adults stay on isolated perches distant from foliage; birds that peck or go short distances for prey in dense foliage have young out at an early age. Short legs make hopping about without using flight difficult in tyrannids.

The females seemed to have no difficulties obtaining large camouflaged insects, even stick-insects and green-leaf mimic katydids to feed the young and themselves. Thus, slow growth of young was not obviously related to lack of food, or to low-quality food. Also, even long periods frozen near the nest on approach, plus monkey and other disturbances, did not result in low food supplies, for rapid sequences of feedings were recorded even at mid-day after long periods off the nest. However, slow feeding rates with slow growth could allow females to wait whenever a predator is around.

Fruit use only late in nestling life, plus bringing 2-3 fruits at a time, may indicate that fruits are so low in food value that they are worth bringing only when rapid feedings are possible, when the young is ready to fly at any

predator approach. Alternatively, big valuable fruits are usually round, and could only be swallowed when the young gape is well grown. Cicadas, round insects with projecting eyes, only entered in the diet at the time fruit use started.

Absolute silence to avoid predators at the nest is favored by having only one young, and may have favored female-only nesting. Otherwise, male and female tend to call to each other, while two young may squeak or otherwise attract attention by active movements in food competition, not the sudden bill opening of the sluggish young piha after a long pause when the female arrives at the nest. The puffing call of the female to lead the fledgling to high in the forest was so whispered and inconspicuous that Willis had to get under both to see which bird was calling.

Eating fecal sacs does avoid nest predation. Carrying the sac away, despite trouble wiping sticky material off the bill, would be necessary with the larger sacs late in nestling life. One female rarely carried sacs, however. Both females dived after falling sacs, even eating them in flight, probably because cats and other intelligent predators might be attracted by sacs that fell to the ground.

Snow (1982) registers that the canopy Rose-collared Piha (*Lipaugus streptophorus*) may be monogamous, since a male was following a nest-building female. This species may be at an early stage in the evolution of nonmonogamy in the genus, or it may be that canopy pihās are more monogamous than midstory ones as would be expected from antipredation hypotheses. Also, cold-climate pihās may have to brood young more, making male help in feeding nestlings more valuable, if it occurs. However, the Rufous Piha brooded its young much more than our pihās, even without male help (Skutch 1969). Beehler (1983b) recorded a monogamous cold-climate bird-of-paradise. Other possible causes for Beehler's record and monogamy in the

Rose-collared Piha could be lack of predators at high elevations, or in more open habitats.

Another case in birds-of-paradise (Beehler 1985) may be explained by low food value of figs used to feed young, raising the value of male help to the point where it offsets the predation disadvantages; however, this bird also seems a canopy species and to occur only in large fruit trees where the mate and other birds can help detect active predators, not "traplining" alone in a dangerous dark forest interior. Also, fig fruits are not scattered, allowing a male to forage next to his female and watch for predators or keep outside males away from her; "foraging circles" of mates are small. Gibbons (Hylobatidae) are similar; a species that eats figs has more infant-carrying help from the nearby male and a "traplining" species less (Palombit 1996).

Discussion of nonmonogamy of the "polygamy" type has paid attention to vegetation and predation, but been linked mostly to food supply – the "polygamy threshold" idea that one male or female sequesters a good site and females or males flock to this "rich" individual, for instance. The idea does not really explain why other individuals can't move in on the "rich" one and cut his or her domain down to a very small size, however. Is there some predation problem, maybe the fact that very dense males or displays attract hawks and raccoons and scare off females?

Beehler indicates that "traplining" birds of paradise seem mostly nonmonogamous, ones grouping in large fruiting trees monogamous. Parrots and other monogamous frugivores also do not trapline, they go to a fruit source and stay rather than move constantly. Probably predation is much more likely on trapliners, including nonmonogamous woodcreepers and cotingines, favoring birds traveling without a mate. Also, the male cannot keep next to his female, and prevent EPC's if each bird needs a large foraging circle, except

in an open habitat where predators, mate and intruding males can be seen far off.

Conclusions on nonmonogamy. Although we recognize that evolutionary scenarios are difficult to prove, we propose that evolution to exploit traped fruits and large insects in the forest interior exposed pihas to dangerous sit-and-wait predators of both adults and nests. Mate guarding became both difficult and dangerous, and males could no longer stop their mates from indulging in “eugenic” extra-conjugal affairs (EPC's) with “hotshot” outside males, either by territorial behavior or by mate-guarding. At the same time or later, small nests with a single young helped to avoid predation, while developmental problems and lesser predation without male visits prevented cutting down the length of nestling periods. Help in feeding young by the males often being of little value or a detriment, females began to attack them, especially near nests – where food supplies might go to males or where their activity could attract the attention of predators. The males, as well as “emancipated,” were “disfranchised”: they had to hunt for “hotspots” (good places for females) and to show off “hotshot” good genes and virility with loud calls, even if their loud calls or displays attracted predators as in frogs (Ryan 1985). Male *L. lanioides* have projecting long 9th primaries, probably used in some kind of wing-whirr display like that of the female attacking *X. albicollis* (Snow 1982: 111).

We thus think that previous ideas on the subject of nonmonogamy in tropical frugivores can be applied to piha evolution, but that casual attention to predation in many earlier accounts has left out a major section of the argument. Also, earlier arguments have rarely paid attention to environmental structure (open versus closed environments) and food or defense strategies of prey and predators (such as salliers vs gleaners, large vs small

foraging circles, traped vs group foragers, sit-and-wait vs mobile hawks and hiding vs mobbing in nest defense). Whereas other forms of nonmonogamy may have followed other evolutionary paths, even grouse (Tetraonidae) in dense but short vegetation may have special predation problems that affect evolution of nonmonogamy.

Weather and brood care. Long rainy periods did force the females to brood more when young were small, and kept them away when young were large. Whether a more rainy normal year would have caused trouble in feeding young is uncertain. The hot summer we worked caused females to gape and preen a lot, perhaps indicating problems of overheating or of ectoparasites. It is likely that this species cannot nest in sunny cutover or patchy forests, where hot sunflecks would overheat the incubating females for long periods on any sunny day. Also, they may avoid forest-edge nesting for similar reasons. We saw them along forest roads, but never in second growth or at open forest edges. This could be one reason why they do not survive in patchy or “Swiss cheese” types of forest zones, only in large forest tracts. However, a nest of similar but heat-adapted (lowland) *Lipaugus vociferans* at Manaus (Willis in Snow 1982) was near the edge of a tall forest plantation.

Road dust at the first nest could have caused some preening, but this would rarely occur in an undisturbed habitat. Preening on the nest, while never very conspicuous, could have attracted predator attention. However, the females always watched carefully and slowly at intervals during preening, and the young bird preened mainly when the female was present to keep a lookout. Later, when about ready to fly, it preened at times when she was absent, but it was already nearly as large as the female, and quite visible on the tiny nest even when sitting. We do not think the female or young preened or turned to give

the impression of a bird off the nest, a behavior noted in monogamous *Iodopleura pipra* (Willis & Oniki 1988). The ant invasion at the second nest did run the female off, but we do not know if such incidents could cause an accidentally broken egg or attacks on eggs or young. The role of ectoparasites is not clear; the birds did seem itchy at times, whether from lice or from body molt is uncertain.

Molt at the time of nesting may allow females to nest two or three times per year, raising annual productivity. Slow growth of tail feathers in female 2 may have indicated arrested molt. If molt causes females to preen more, however, this could attract predators to the nest.

Sunny edges. Our nesting studies indicated some overheating of birds in the unusually hot summer of 1995. In 1996, there was a second hot and dry summer at Santa Teresa. If greenhouse effects start to increase summer temperatures and droughts, drying out the montane forests, or if forest edges continue to spread with human occupation, *L. lanioides* – a bird of limited distribution that survives only in large uninterrupted forest tracts – could become even less common.

Forest edges and hot summers cause many effects (including sun and dust problems, wind damage, and invasion of *Buteo mag-nirostris* hawks along roads at Nova Lombardia in the hot summer of 1994–1995), that would repay ecological and physiological study. In March 1995, at nest-2, local farmers “donated” their work to cut understory roadside vegetation back almost to the nest, so as to get more than enough room for their small trucks to pass, yet reserve managers made no objections. Nest-3 was almost over the road, in a sapling of the same size as some cut unnecessarily by these over-enthusiastic farmers.

We hope that paving and widening the roads (except in future tunnels) will not be

permitted in the reserve. Even invasions of public or private property by poor farmers (“sem terra”) occur in Brazil, supported by “good” organizations like churches and anthropologists or sociologists, resulting in destruction of forests and savannas (areas called “unproductive” by many farmers, churches, local groups, and political parties). As in many other countries, it is difficult to avoid creating edges, or to slow down destruction of natural habitats. A large part of the problem is that “productivity” and “good” are defined by developmentalists of religious and political sects, “homocentric” groups that rarely pay attention to environmental problems.

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