ABSTRACT.—I studied the White-bearded Flycatcher (Conopias inornata = Myiozetetes inornatus) in Venezuela during its breeding season. Its nest was a small open cup covered on the exterior with applied lichens. The natal down was dense, short, and pale yellow. A single extra parental helper was found in two of the three territories studied. All members of these closely integrated social groups built the nests, fed the nestlings, and defended the territories. Incubation and brooding were shared by both sexes and sometimes by the helper. The White-bearded Flycatcher duetted antiphonally. It was parasitized by the Shiny Cowbird, Molothrus bonariensis. Conopias inornata nest structure, nestling down, and male breeding behavior differed from those of Myiozetetes cayanensis, M. granadensis, and M. similis. These differences support the use of the genus Conopias in place of Myiozetetes. Received 3 November 1978, accepted 6 July 1979.

BEHAVIOR AND BREEDING OF THE WHITE-BEARDED FLYCATCHER (CONOPIAS INORNATA)

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STUDY AREA AND METHODS

All observations were made on Fundo Pecuario Masaguaral, a cattle ranch located at 08°31'N 67°35'W, which is near the middle of the Venezuelan llanos, in the state of Guárico. The llanos are low-elevation, flat grasslands with scattered trees and palms, interspersed with occasional forest patches and small clumps of trees and bushes. The area is regularly subjected to about 6 months of rainfall, May–November, and 6 dry months. The annual mean rainfall is 1,483 mm (n = 24 yr). A more detailed description of the study area and an annotated list of its birds is given in Thomas (1979).

I observed the birds from March through September 1977 and supplemented my observations with some notes from 1976 and 1979. I mist-netted adult members of three adjacent territorial groups and marked them with colored plastic bands. Later I color-banded their nestlings. Observations were made with 8 × 32 binoculars, without a blind. The birds readily accepted a seated figure, which gave me an unrestricted view and made it possible to continue observations at midday air temperatures over 35°C. Field notes were either written directly or dictated into a portable cassette recorder. Measurements were made with a vernier caliper graduated to the nearest 0.1 mm, with 10- and 50-g Pesola spring balances,
and with a stopwatch. Plumage and soft-part colors were compared in the hand with color swatches (Smithe 1975). Sometimes I used taped vocalizations to locate banded birds. Field recordings were made with a Uher 4000 Report-IC Automatic tape recorder and a Dan Gibson 18-in parabolic reflector. Sonograph analysis was done on a Kay Elemetric Sona-Graph 7029A using a wide band filter.

RESULTS

ADULTS

Description.—The White-bearded Flycatcher (hereafter called inornata) is monomorphic. Adults weigh 29.5 g (27.0–31.5, n = 18). The back, wings, and tail are olive brown (#28 of Smithe 1975) and the underparts are spectrum yellow (#55). A wide white superciliary line completely circles the head. The crown and sides of the head are dusky brown (#19), clearly darker than the back. Irides are burnt umber (#22), and the bill, legs, and feet are black. The chin and throat are white, as the common name implies, but this is not a conspicuous field mark; more appropriate is the name inornata because similar flycatchers have brightly colored crests, usually concealed, while neither sex of inornata has a colored crest.

Beginning in August, at the end of the breeding season, adults molted remiges in the usual order, but rectrices were molted centripetally, starting with the outer tail feathers and finishing with the central pair.

Distribution.—Inornata is reported to occur in suitable habitat from the Venezuelan coast south through the llanos, including the south side of the Orinoco River (Phelps and Phelps 1963, Meyer de Schauensee 1966, Meyer de Schauensee and Phelps 1978). It is found at elevations below 500 m in small groups of trees and wooded copse.

Social groups.—In two of the three territories that I studied the pair had a single helper. These helpers were banded as adult-sized birds prior to the breeding season. Helpers greatly assisted the pairs in nest construction, nestling feeding, and territory defense. Helpers also incubated eggs and brooded nestlings but less often and for much shorter periods of time than did the pairs. Details of helper assistance will be reported later. In both territories with helpers, cooperation among the three adult birds was very close; at no time was there any antagonism to the helpers. No copulations were observed, but the pairs, or principals, were determined by their nearly equal share in diurnal incubation and brooding. The relationship of the helpers to the pairs has not yet been resolved.

Foraging behavior.—Pairs and small family parties forage from low to medium-height perches (\( \bar{x} = 1.4 \) m, 0.15–4 m, n = 39) in shaded open understory. They watch the ground intently for invertebrates, then fly down directly for the prey, returning to a different perch before eating the prey. When inornata fails to capture prey, it hops around, reaching under leaf litter with its bill. Less often inornata flycatches in the air by darting out to capture flying insects. Incubating and brooding birds fly off the nest to catch prey opportunistically, either to eat the prey or, more frequently, to feed nestlings.

During the wet season over half of the area in each of the three territories I watched was flooded 5–50 cm deep. At this time more foraging was done in the air and at grass-top level, and the prey size was smaller, probably reflecting the seasonal increase of mosquitos and other dipterans. Occasionally inornata flew down to pick prey from the upper surface of leaves, as described by Skutch (1972: 151) for Conopias parva (=Coryphotriccus albovittatus). Most prey items were too small to be
recognized, but the larger invertebrates that \textit{inornata} ate or fed to nestlings were (in the order of frequency seen) caterpillars, adult lepidoptera, spiders, crickets, centipedes, beetles, and roaches. Large prey, especially some caterpillars and centipedes, were beaten repeatedly against the perch before being eaten.

Infrequently \textit{inornata} eats fruit. Once, late in a nestling feeding cycle, one of the principals and the helper ate a few small berries. This may have been substitute feeding, because the preferred food, invertebrates, was fed to the nestlings. Perhaps fruit, an accessible but less nutritious food, was eaten for self-maintenance (see Morton 1977: 102). After the first brief rains, individuals drank from leaves and bathed by flying into and fluttering against wet leaves.

\textit{Vocalizations}.—The common call, a sharp rising \textit{churup} (Fig. 1A), is used by all members of the social group. Single \textit{churups} seem to serve as location calls, often being answered by another member of the group, while repeated \textit{churups} appear to be a warning. In strong defense, against both intraspecifics and interspecifics, two birds give an explosive, antiphonal duet (Fig. 1B). While duetting, they rapidly pump their bodies up and down as they snap their wings rhythmically. If a nest is being defended, the covering bird sometimes gives its part of the duet, including the physical display, on the nest. More often \textit{inornata} flies to perch 10–20 cm from its mate to duet in the nest tree. Duetting also occurs during the first morning nest exchange by members of a pair, usually near the nest. After the breeding season, duets are given at dawn when a pair or social group leaves its roost tree. Birds also duet as they forage in their territory. Occasionally two pairs with adjacent territories face each other across the territory boundary and duet at the same time.

\textit{Territories}.—\textit{Inornata} responds rapidly to tape recorded duet playbacks. Territorial pairs fly into the tree nearest to the sound source and usually duet. I mapped the approximate territories of the three social groups I observed by noting the points where marked birds frequently fed and duetted. Territorial boundaries often coincided with the perimeters of small, closed-canopy tree and bush clumps. These clumps covered about 30\% of each territory; the other 70\% was open grassland (Fig. 2). The mean size of the three territories was 2.45 ha (2.07–2.88 ha). When an \textit{inornata} that is not a member of the territorial group is found, the residents duet and chase it aggressively. The Dwarf Cuckoo (\textit{Coccyzus pumilus}) sometimes responded to \textit{inornata} playback duets during its breeding season; the two species' vocalizations are similar (Thomas 1978).

\textbf{Breeding Biology}

\textit{Nest and eggs}.—Nesting begins in late March, near the end of the dry season, and nests are placed in sun-exposed sites. The nests are usually on horizontal forks
Fig. 2. Territories of the study birds. Numbered circles indicate the places and order of nests. Tangent circles indicate nests built in the same tree. Territories Orange and Red each had one adult helper; territory Green had no helper. Stippled areas represent tree clumps and bushes, open areas are grassland.

of tree branches and cryptically concealed on the exterior with applied lichens (Fig. 3B). The typical nest is a small, shallow open cup, about 8 cm outside and 5 cm inside diameter, with an interior depth of about 2 cm. A voucher specimen has been deposited with the American Museum of Natural History. The mean height of 13 nests was 6 m (3–13 m). All were in smooth-barked trees: matapalo (Ficus spp.), caruto (Genipa americana), carocaro (Enterolobium cyclocarpum), coco de mono (Lecythis ollaria), and maremare (Cassia grandis).

The nest is constructed of fine petioles, rootlets, tendrils, bits of leaf skeletons, and occasionally a few small feathers. One nest was lined with black horsehair. The material is held together with spider web. Gradually the exterior lichens dry and become white dots, by which time the nestlings also have a strong light and dark aspect. Thus the lichens may serve to camouflage the growing young. Both members of the pair and the helper build the nest. They take turns crouching inside and turning around while they press and shape the nest with their feet and breast inside and their wings and tail outside of the cup. This results in a tightly matted thick rim. Selection for very similar body size of the two sexes may be important for this type of cooperative nest construction.

Replacement nests are started by the pair or social group a few days after eggs or young have suffered predation. Nearly all of the material in the old nest is carried to the new site, except for the lichens, which are torn off and dropped below the old nest. New material in replacement nests is mostly spider web and fresh lichens on the nest exterior.

An open cup inornata nest with two eggs was reported by Cherrie (1916: 238). I found clutches of two eggs in 12 nests. The eggs are oblong oval (Pitman 1964)
and white with a few scattered dots and blotches up to 3 mm wide of chestnut (#32), mostly at the larger end. Mean weight of 5 eggs was 3.4 g (2.8–4.15 g), and they measured 23.5 × 17.1 mm (21.7–25.0 × 16.4–17.9 mm). Eggs were laid on alternate days and from early April to mid-July.

Incubation. —Incubation is started with the laying of the first egg. The incubation period from the day the second egg was laid until the hatching of the last egg was 17 to 18 days. I recorded the behavior of the attending trio of birds from 0600 to 1900 on the day before the first egg hatched at Orange territory nest #1 (Figs. 2 and 3A). The same individual of this social group always covered the nests in this territory at night and was still on them at dawn. I assumed that this was the female. Nest attentiveness, incubation periods, and duets are shown in Fig. 4. The presumed male flew into the nest tree and churuped at 0655. At 0708 the pair performed their
first duet; the first nest exchange followed. On this morning there may have been one or more extra duets because of my presence; otherwise the day’s behavior was generally representative of that observed at two other nests.

When ambient temperature was over 34°C, nest coverage approached 100%. During exchanges at this time, the incubating bird flew off only as it saw the relieving bird flying toward the nest. Midday to early afternoon incubation sessions were generally shorter than those of morning and evening (Fig. 4). Recesses in the early morning and late afternoon suggest that the eggs were being protected from dehydration or heat, not chill (see Drent 1975: 359–363, Yom-Tov et al. 1978). These recesses were taken during times of little or no wind, however, when the danger of egg loss from buffeting of the shallow nest by the brisk diurnal wind is minimal. There were 32 nest exchanges during the 13 daylight hours, and the nest was covered 94% of the time, 47% by the male, 45% by the female, and 2% by the helper. The helper, in a single visit, crouched over the eggs for 14.5 min rather than sitting fully down on them. The relieving bird made no unusual response when it returned and found the helper on the nest.

Nestlings.—On the morning of 23 April the first egg hatched at Orange nest #1. The incubating bird, the presumed male, repeatedly stood up and picked at the nest and at 0847 flew 2 m away with half a shell, which it nibbled until the wind blew the shell away. Meanwhile its mate had covered the nest. At 0850 the pair met near
the nest, duetted, and the male returned to brooding. At 0851 the female brought the first food, a 2-cm green caterpillar. The male left, but the nestling did not gape, so the female brooded while holding the food. The second egg in this nest hatched on the following day.

Seven hours after hatching, the nestling (Fig. 3C) weighed 3.3 g; its eyelids were closed and it peeped weakly. The bill was dark orange yellow (#18) with a blackish tip and a white egg tooth. The body was dark spectrum orange (#17), the legs and feet orange yellow (#18). It had dense, short, pale yellow down. In the capital area (nomenclature follows Wetherbee 1957), the orbital, coronal, and occipital tracts had much down. Some down was present in the auricular and post auricular areas. The spinal tract had down in the scapular, femoral, dorsal, and pelvic areas. The alar tract had down on the patagium and secondaries and their coverts, but the details of distribution in this area were not determined. Down was also present on the abdominal region of the ventral tract. Wetherbee (1957: 404) suggests that a large amount of down is adaptive for species nesting in sun-exposed nesting sites.

At the ages of 4 and 5 days (Fig. 3D) the two young of this nest weighed 9.6 and 11.8 g. Their eyelids were still closed, and their sharp claws clung tightly to the nest lining. The legs and feet were pale buff (#24), and the skin color had changed to dark grayish brown (#20) dorsally and to tawny (#38) ventrally. Two wide tracts of emerging ventral feather quills were close to spectrum yellow (#55). These quills covered the interramal, malar, submalar, cervical, sternal, and auxillar tracts, meeting the abdominal region down (nomenclature from Van Tyne and Berger 1959). The primaries and secondaries and their coverts were emerging quills. The bills were black with bright yellow rictal flanges. The nestlings made weak sounds, but they could not turn over when laid on their backs.

On days 9 and 10 (Fig. 3E) these nestlings weighed 12.3 and 16.2 g. The primaries, secondaries and coverts of the younger bird were still in their sheaths; those of the older bird were emerging. The eyes of both birds were open and the irides dark. The gape was spectrum orange (#17) with the rictal flanges changed to pale yellow. I could not see or feel an egg tooth. The ventral feathers had emerged and showed the same yellow as in adults. The legs and feet were flesh color (#5). Late on days 14 and 15, the nestlings were taken by a predator. Two days later the helper of this social group also disappeared.

Nestling care.—Parents shared the brooding of nestlings, and occasionally helpers brooded briefly. All three adults of both territories with helpers fed the young. During 33 h of observations at two nests, the presumed male parents made 31% of the feedings, the presumed females made 44%, and helpers made 24%. Frequently the helper foraged within a meter of one of the principals, and it often perched less than 15 cm from them.

The nestlings were extremely docile. Often adults lingered on the edge or beside the nest with food, waiting for them to gape. Any bird covering the nest when another arrived with food flew off promptly. When two birds came at the same time, one waited a short distance away while the other delivered food. All three adults maintained nest sanitation. The parents either ate fecal sacs or carried them to the perimeter of the nest tree and dropped them. The helper carried them away and dropped them. The nestling period was found to be 18 days at one nest.

Postfledging period.—A helper also assisted at Red nest #2 (Fig. 2), where two young fledged. I continued to observe these five birds for about 2 months after the
fledging. At the age of about 4 weeks the fledglings flew well for short distances, but they spent most of the time perched together where their parents brought food to them. In a total of 14 h observation I did not see the helper feed the young, although it remained with the four, assisting in defense of the fledglings and the territory. One young bird scratched its head indirectly (over the wing) in the manner of the adults. One fledgling made the first part of the churup call, but not the full adult vocalization.

On about their 32nd day the juveniles allopreened, both by picking at body feathers and by nibbling progressively along the remiges and rectrices of the sibling. By their 46th day, both young began to fly down to the ground in foraging attempts, but they were still largely dependent on their parents for food. During the next 2 weeks one of the young birds disappeared. At the age of 3 months the other juvenile foraged successfully, but it still followed and begged from the female parent. The remaining four birds of this social group continued to roost together and they spent their day foraging near each other within their territory.

Renesting.—The Orange pair, which lost its first nestlings early in May, made three renesting attempts, in late May, mid-June, and mid-July (Fig. 2). Each subsequent nest was parasitized by the Shiny Cowbird (Molothrus bonariensis); none of these nests fledged either an inornata or a cowbird. Pair Red lost its first nest to an unknown cause and fledged two young from a second nest. Pair Green, which was not assisted by a helper, lost two eggs from its first nest, lost two nestlings from a second nest, and fed a single cowbird in a third nest. The interval between the loss of eggs or young in a nest until the first egg was laid in a replacement nest was 10 days.

**DISCUSSION**

Like *inornata*, some other tropical tyrannids often are found in small groups: *Myiozetetes granadensis* and *M. similis* in Peru (Fitzpatrick pers. comm.) and *Conopias parva* in Costa Rica (Skutch pers. comm.). Intraspecific "intruders," which perhaps were helpers, have been reported for *Tyrannus tyrannus* (Smith 1966: 10) and for *Myiozetetes similis* (Smith pers. comm.). The relationship and role of the *inornata* helper and of cowbird parasitism must be examined in a larger sample before conclusions can be drawn about their effects on social structure and breeding success.

The *inornata* nest structure is entirely different from the large, conspicuous, covered nest of dry grasses built by *Myiozetetes* species (Cherrie 1916, Skutch 1960, Haverschmidt 1968, Wetmore 1972). Both sexes of *inornata* build the nest, incubate, and brood the nestlings. In *Myiozetetes* these are reported to be done by the female alone, except for one report of nest building by both sexes in *M. cayanensis* (Haverschmidt 1968). The *inornata* natal down is abundant and dense, covering much of the nestling at hatching. Skutch (1960: 441 and 418) has reported "sparse light gray down" for both *Myiozetetes granadensis* and *M. similis*. Hatching *M. cayanensis* has only scattered down on the dorsal area (pers. obs.). Thus, *inornata* nest structure, male building, incubating, and brooding, as well as natal down, are all very different from *Myiozetetes*, strongly suggesting that *inornata* may not be taxonomically close to *Myiozetetes*. This supports Traylor (1977: 167–169), who retains *inornata* in *Conopias*. 
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LITERATURE CITED


