LIFE STYLE OF *COCCYZUS PUMILUS*, A TROPICAL CUCKOO

CAROL PEARSON RALPH[1]

Departamento de Biología
Universidad del Valle
Cali, Colombia

Within the cuckoo family, Cuculidae, are brood parasites, communal nesters, and polyandrous species. One member of the Cuculidae, the Dwarf Cuckoo (*Coccyzus pumilus*), may have an unusual breeding system that might demonstrate traits that would clarify the evolution of other breeding systems in this family. Also, since *C. pumilus* is tropical and has two closely related temperate-zone counterparts for comparison, it can be used to test current generalizations about tropical vs. temperate adaptations. It can be considered an opportunistic species, exploiting caterpillar outbreaks, and a colonizing species, expanding its range as man creates habitat suitable for it. A life history of *C. pumilus*, then, is potentially more than a simple addition to our knowledge of the rich, but still relatively undocumented, avifauna of the American tropics.

THE BIRD, ITS RANGE, AND ITS HABITAT

C. pumilus, weighing about 36 g, is smaller than other *Coccyzus* and has a rounded rather than a graduated tail (fig. 1). In the adult the chin, throat, and upper breast are a rich rust color; the upperparts, wings, and tail are smooth brownish gray; and the abdomen is white or buff. The iris and orbital skin are permanently bright red. The sexes are indistinguishable by plumage. In this study birds were sexed by behavior during copulation. In the juvenal plumage the upperparts and flight feathers have a tannish cast, and the throat is pearly gray. The iris is olive brown, the orbital skin is yellowish, and the mouth lining is pinkish, turning black with age.

The basic range of *C. pumilus* is northern Venezuela and northern Colombia (Meyer de Schauensee 1964) from sea level to about 2000 m altitude in zones mapped as Tropical and Subtropical Dry Forest (Espinal and Montenegro 1963). As a bird of open woods in these zones (Meyer de Schauensee 1964), it has adapted well to man's tree-lined pastures, orchards, gardens, and cleared forests.

In Colombia, the most recent records extend the range farther south. In many cases these southern areas were previously unsuit-

able for *C. pumilus* or inaccessible to it. In 1943 *C. pumilus* was collected at 2600 m in Bogotá (Borrero 1946), and in 1966 it was reported in the upper Magdalena Valley (Nicéforo María and Olivares 1966); both areas are separated from the main cuckoo population in the north by small barriers of more humid habitat. A larger barrier of wet forest separates the Tropical and Subtropical Dry Forests of the upper Cauca Valley from the northern center. About 1870 timber cutting began to break up this forest barrier (V. M. Patiño, pers. comm.), opening the way for the cuckoos to the upper valley. Also, land improvement for pastures and plantations in the valley (Crist 1952; V. M. Patiño, pers. comm.) improved the habitat for Dwarf Cuckoos. By 1956 *C. pumilus* was near Cali (Lehmann 1957). More recently it was recorded on the western edge of the Amazon rainforest in Florencia (Nicéforo María and Olivares 1966). In 1971 I found *C. pumilus* in Buenaventura, on the very wet Pacific coast (Ralph and Chaplin 1973). Here it was breeding in a small area of shrubby pasture and orchard cleared from the forest. Both these wet forest sites are separated from dry forest *C. pumilus* populations by high, wet ranges of the Andes. Probably the clearing of forests along roads over mountain ranges and in the associated towns has opened the way to these new areas, which are now suitable for cuckoos.

STUDY AREA AND METHODS

I studied a population of *C. pumilus* near Cali, Colombia, 3° N, in the valley of the Río Cauca at 1000 m altitude. By the Holdridge classification, the area is Tropical Dry Forest (Espinal and Montenegro 1963). In some years distinct dry seasons do occur here, but during the year of this study rain fell in all months (fig. 2), and any rainy or dry "seasons" were short. Total precipitation from July 1970 through August 1971 was 184 cm. The temperature varies little during the year. The extremes for August 1970 through August 1971 were 12.9°C and 32.6°C, and the daily average was 22.7°C. (Weather data were supplied by the Corporación del Valle del Cauca.)

The area most intensively studied was roughly 29 ha (72 acres) on the lowest foothills of the Farallones de Cali in the drainage of the Río Pance. This area is pasture land (fig. 3) broken by rows and clumps of trees, both along fences and in the gardens of scattered suburban homes. The three most common trees here, which are also the substrate of most *C. pumilus*

FIGURE 1.   An adult *Coccyzus pumilus*.

FIGURE 3.   Pasture habitat of the study area. In foreground is a *Fagara* used as a nest tree. Note clumps of mistletoe.

activity, are all small to moderate-sized species: the chiminango (*Pithecellobium dulce*—Mimosaceae) and ūna-de-gato (*Fagara* sp.—Rutaceae), both as naturally dispersed trees, and mataratón (*Gliricidia sepium*—Fabaceae), planted as fenceposts. Citrus trees, planted in small orchards or gardens, also are common.

On this study area, between July 1970 and August 1971, I color-banded 18 adult and 13 juvenile *C. pumilus*. Of these, nine adults were resident on the study area, and I followed them closely for 7 months (15 January–15 August 1971). I supplemented the colored leg bands of these nine birds and their offspring with spots of quick-drying enamel paint on the rectrices or remiges. I visited the study area on the average 4.4 days per week to check nests and record locations of any individuals seen. Each visit usually lasted 2–5 hr, and the total time spent in the field was roughly 550 hr. I spent about 175 hr making observations at 18 different nests rather than following foraging birds. Most observation periods
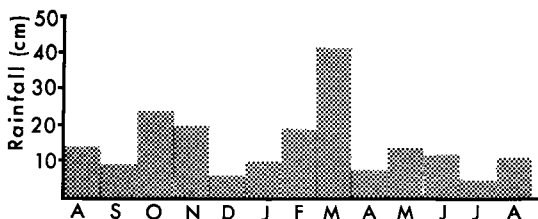
at nests were 2 hr long. Since blinds placed near nests often disturbed the adults, I usually observed nests from a distance of 8–50 m from the nest, without a blind. To minimize disturbance of the nests I spent only about 1 min at a nest while checking its contents, using a mirror on a pole where necessary. I banded the young at about 12 days of age, just before their first flight.

During the study period I found 27 nests, most on the study area. I had found and observed three additional nests between 5 August and 8 September 1970. Local residents helpfully provided observations on a few nests. Five nests whose destruction or desertion probably was caused by my activities were omitted from nest-success calculations.

FOOD AND FORAGING

Like other *Coccyzus*, *C. pumilus* forages slowly, peering about for large prey items. It frequents both outer and inner branches of trees and descends onto clear ground under trees and into dense grass and bushes. Chiminango and mataratón seem to be the trees most frequently used. During this study mataratón often hosted many tortricid and noctuid caterpillars. The main item of the *C. pumilus* diet in the Cali area is the caterpillar (table 1). Since the caterpillars eaten averaged about 0.04 g dry weight, and the membracids, which were mostly nymphs, only 0.02 g, the caterpillars are even more important than this table shows.

The caterpillars eaten range from tiny leaf-tying, nest-building tortricids about 13 mm long to large arctiids 51 mm long. The most common caterpillars in the stomachs were noctuids, probably *Azeta*, 27–48 mm long. These were not very bristly or otherwise known to be obnoxious. However, some of the arctiid caterpillars eaten were quite hairy, the lampyrids (lightning bugs) were distasteful, and the membracids (treehoppers) have

FIGURE 2.   Rainfall in Cali from August 1970 through August 1971.

TABLE 1. Relative numbers of food items of *C. pumilus*, based on observations over the entire study period.

Food item	Observed eaten by adults	In stomachs of adults[a]	Observed fed to young
Caterpillars	150 (60.0%)	119 (60.7%)	115 (54.8%)
Treehoppers (Membracidae)	90 (36.0%)	61 (31.1%)[b]	0
Moth	1 (0.4%)	0	2 (1.0%)
Dragonfly or cicada	1 (0.4%)	0	0
Unidentified insects	8 (3.2%)	6 (3.1%)	93 (44.3%)[c]
Lampyrid and other beetles	0	10 (5.1%)	0
Total sample	250	196	210

[a] Six adults collected within 2 km of the study area. Stomachs of all six contained caterpillars; three contained treehoppers.
[b] Mostly nymphs.
[c] Probably all caterpillars.

several spiny projections. *C. pumilus* obviously confirms the cuckoo tradition of eating distasteful or uncomfortable food (e.g., Forbush 1927).

C. erythropthalmus and *C. americanus* eat large numbers of tent caterpillars (*Malacosoma*), even to the point of reducing outbreaks (Forbush 1927). In contrast, I saw *C. pumilus* pecking at the web and leaf nests of tortricids only rarely, and then only gingerly.

Cuckoos often shake and mandibulate their food before swallowing it or feeding it to nestlings. This process could serve to shear off the hairs and perhaps to shake off any defensive secretions of the caterpillar. However, J. I. Borrero (pers. comm.) has observed *C. pumilus* squeeze out the contents of caterpillars by mandibulation and then swallow the still bristly skin. Also, fully furred larvae occur in the gizzards, along with spiny membracids. North American cuckoos shed the lining of their gizzards, presumably to clean them of embedded hairs and bristles (McAtee 1917). In three out of six *C. pumilus* examined, I found a loose gizzard lining, indicating it is shed in this species also.

HOME RANGE AND RESTRICTED DOMINANCE AREAS

Pasture land is a heterogeneous habitat, where trees suitable for foraging are widely dispersed. In this situation individual cuckoos have large home ranges. I determined minimal home ranges by mapping all sightings of marked individuals over the 7 months and connecting peripheral points to form polygons with all internal angles less than 180° (fig. 4). Most pairs ranged off the study area to some extent. The largest home range measured, and probably the most complete, was the 10.0-ha (24.7 acres) range of Pair IA. Some large passerines have territories or home ranges of about this size (Schoener 1968).

Sightings away from the nest area were too few to reveal temporal changes in home ranges, but in general birds were seen at the edges of their home ranges during all nesting stages. Also, both members of a pair covered about the same terrain.

Figure 4 shows that home ranges overlap greatly. Most foraging sites were used in common by at least two pairs, although not simultaneously. In these "commons" I occasionally saw one bird fly after another, one or both giving the sputter-*churr*, a stuttering, interrupted version of the *churr* (described below). However, chases like these were also part of courtship, so they were not necessarily boundary disputes.

Defense of the nest area was more intense. Birds going to or from the nest occasionally supplanted and chased intruders that were
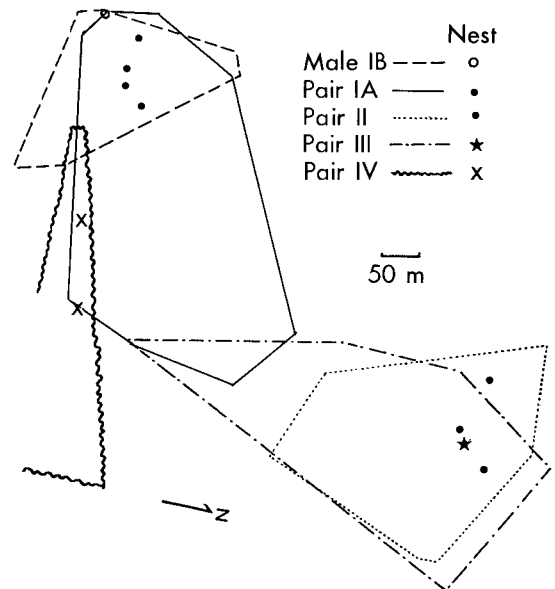

FIGURE 4. Nest sites and partial home ranges of four pairs and a second mate of Female I over the 7-month study period. The home ranges cover almost the entire study area, about 29 ha.

within 10–20 m of the nest and often chased those found in the nest tree. However, incubating birds did not chase intruders. On four occasions I saw an incubating bird ignore an alien *C. pumilus* in the nest tree. Since the adults spend most of their nonincubating time far from the nest, visiting it infrequently (see below), an intruder often can approach the nest. In other words, nest area defense is serious, if the owner is near the nest but not on it; however, this is often not the case, so defense is ineffective.

This lax defense of the area around the nest permits neighboring pairs to build nests quite near each other (fig. 4). In five cases a pair built its nest within 40 m or in plain sight of another pair already incubating or feeding. Also, pairs tended to renest near their previous nest. Nests seemed to be more clumped than were suitable nest trees.

Related to this lack of well-defended territory was an apparent absence of advertising song. The only loud vocalization I heard from *C. pumilus* was the *churr* call, a grating *trrr trrr trrr . . .*, usually 4 to 25 syllables, given at about one syllable per second. For reasons given below, I interpret the *churr* as a call to maintain pair contact. The *churr* is given in many of the same situations as the *kowlp* call that Hamilton and Hamilton (1965) described for *C. americanus*. They interpreted the *kowlp* call as a possible spacing mechanism. They suggested the *coo* call, given from exposed perches in long bouts, was an advertisement song. In *C. pumilus* in Cali I found no equivalent to the *coo* call. In Venezuela, P. Schwartz on one occasion (at dawn) heard and recorded a *kööa-kööa* song of *C. pumilus* (Neotropical Institute, *Coccyzus pumilus*, Cut 1 in Cornell Laboratory of Ornithology, Library of Natural Sounds).

PAIR RELATIONS

The function of the *churr* as a call to maintain pair contact is indicated by its context and its development. Birds of both sexes *churr* at irregular intervals while foraging and when traveling to or from the nest. They often take flight just after *churr*ing but also *churr* while flying. A perched bird may *churr* while hidden in foliage or while exposed at the treetop. Frequency of *churr*ing by the cuckoos on the study area varied from one or two *churr*s in an entire afternoon to dozens in 1 hr, but I found no apparent relation of *churr*ing frequency with the time of day, weather, or season. A bird on the nest sometimes *churr*s in response to a *churr* of an arriving mate and sometimes

*churr*s without any apparent stimulus. The location note given by young birds is a soft, short *churr*. Probably the adult *churr* develops from this short *churr* and, like it, maintains contact between individuals.

Other male-female interactions I observed were courtship feeding, mounting of the female by the male, and copulation. I observed courtship feeding by pairs in all stages of nesting. Mounting, however brief, always followed courtship feeding. Of the 20 mountings I observed, only 4 went to completion with copulation. In only one case did a male attempt to mount a female without bringing her food. This was a pair without a nest in progress. A courtship encounter begins when the male, bringing a caterpillar in his beak, approaches the female. If the female is on the nest, she leaves it. Often both birds give the sputter-*churr* as they approach each other. If the female is receptive, she crouches slightly, holding her quivering wings away from her body. The male hops on her back, at the same time allowing her to bite the caterpillar so they both are holding it. After a few seconds, or up to 25 sec, the male pumps and rotates his tail and slides partially off to one side so that their cloacas are in contact. The birds hold this position a few seconds, and then the male dismounts, leaving the caterpillar for the female to eat. Sometimes more sputtering and a short chase ensue. Occasionally, before the male mounts or after he dismounts, the two birds perch side by side, each holding onto the caterpillar in a stationary "tug-of-war" for up to 2 min. If the female is not receptive, that is, does not crouch for the male, he will mount and stay on her back a fraction of a second to a half minute without attempting cloacal contact. While a female is incubating or brooding, a male may bring her food, offered in courtship, as often as three times an hour. Such frequent solicitations could contribute significantly to the female's food intake.

Similar courtship feeding is practiced by many other cuckoos, for example, *C. americanus* (Bent 1940), *C. erythropthalmus* (Spencer 1943), *C. melacoryphus* (J. I. Borrero, pers. comm.), and *Crotophaga ani* (Köster 1971).

The members of the four pairs studied were faithful to each other in the sense that they stayed together for the entire 7-month study, through nest failures, renestings, second nestings, and non-nesting periods. More importantly, if courtship feeding is an indication of readiness to breed, they were apparently ready to breed at any time.

FIGURE 5. Nest with nestlings on day 4 and day 5. The nest has excrement accumulated on it. The nestlings show the white spots and bumps on the roof of the mouth and the hair-like first feathers.

NEST CONSTRUCTION

Both sexes participate in nest-building. When the nest is still quite scanty, 2–4 days after construction begins, the eggs are laid and incubation begins. Most construction, therefore, takes place during early incubation. It tapers off and usually ends in the first days after the eggs hatch. Almost all of the nest material I saw added to nests was brought by a bird arriving to relieve its mate at incubation or brooding. If the sitting bird did not quit the nest, the arriving bird passed the twig to the mate for it to add to the nest. The only two intensive bouts of nest-building I witnessed involved one male on one afternoon. He brought eight twigs in one 18-min period and five twigs in a 12-min period. In these bouts he gave the twigs to the female to add to the nest. Similar nest-building behavior is reported for a variety of other cuckoos, e.g., C. americanus (Bent 1940) and the Squirrel Cuckoo (Piaya cayana) (Skutch 1966).

The nest of C. pumilus is rather flimsy (fig. 5). It is a slightly dished platform 10–15 cm in diameter, made of relatively large twigs (6–13 cm long and 1–3 mm diameter), dried tendrils, and occasional long plant fibers. The smaller twigs are added last. Spines or knobs on these twigs, as well as on the branches of the nest tree, help hold the nest together. Some nests have a dry leaf or two for lining. The nests of C. americanus and C. erythropthalmus are similar but usually have more lining (Bent 1940; Spencer 1943; Hamilton and Hamilton 1965).

The nests are usually in the canopy of a short tree, averaging 2.6 m above the ground (n = 29 nests, mode 2.0 m, range 1–6.5 m). Of 30 nests, 16 were in Fagara or Fagara intertwined with another species, 10 were in citrus trees, and 4 were in other species. Of those in Fagara or citrus, four were in mistle-toe (Loranthaceae) and five on small bromeliads (Tillandsia recurvata) in these trees. The nest trees usually are isolated, or face an open area, and the nest is located so that the bird on the nest has a view of the area around the tree. A nest and the ground below it are soon splattered with the excreta of the incubating birds. The nestlings later add to this splattering, making the nest area conspicuous.

EGG-LAYING AND INCUBATION

As mentioned above, the first egg is laid 2–4 days after nest construction begins. The second egg usually follows on the next day, but as many as 3 days may elapse between successive eggs.

Assuming that the eggs in one nest are all from one female, the clutch is of two or three eggs ($\bar{x} = 2.2$, $n = 24$ clutches). However, one female is capable of laying more eggs than the usual clutch. Female IA laid four eggs in 6 days, two in each of two nests.

Several observations suggest that C. pumilus females may lay eggs in nests of other females. In one nest two eggs appeared on the same day. It is unlikely both eggs were from the same female. Twice, unknown individuals were seen very near nests of marked birds during incubation. These could have been females looking for nests in which to lay. Once, an egg was found on bare ground among a few twigs, not near any nest from which it could have fallen. Perhaps this stray egg was left by a female that had not provided a nest at the proper time.

The eggs are oval and white, with a dull white surface that rubs off. They average 24.9 × 19.6 mm ($n = 9$).

Incubation starts with the first egg, initiating asynchronous development of the young in the clutch.

PARENTAL CARE OF EGGS AND YOUNG

At the two nests watched most closely, both parents shared equally in incubating eggs and shading, brooding, and feeding the young during the day. Like other Coccyzus (Kendeigh 1952), C. pumilus has long attentive periods and a low feeding rate at the nest. Incubation sessions tend to be longer than brooding sessions. Eight incubation sessions observed from beginning to end ranged 30–156 min ($\bar{x} = 77$ min), but 41 brooding sessions of young nestlings ranged 3–75 min ($\bar{x} = 23$ min). Brooding sessions of less than 5 min were common, but most brooding sessions lasted 20–25 min. The parents kept the nest covered, warming or shading it almost continuously throughout incubation, and only slightly less for about the
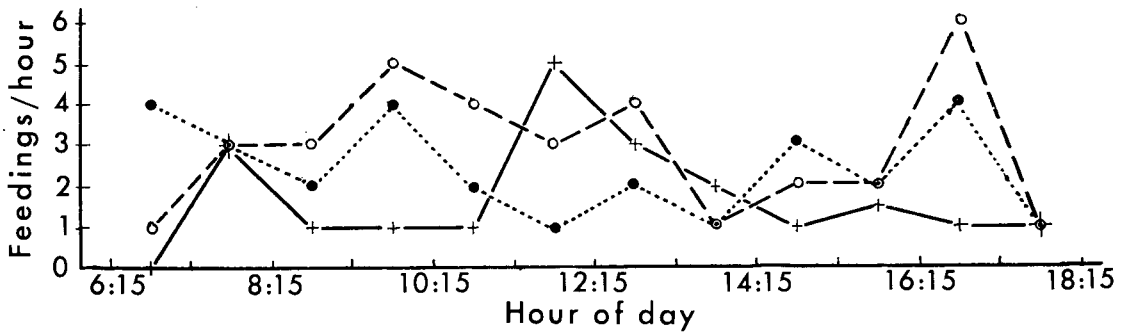
FIGURE 6. Hourly feeding rates over 24 hr at a nest of Pair IA with one nestling on days 7–8 (+) and on day 12 (•), and a nest of Pair III with two nestlings on day 6 (o).

first 4 days after hatching. During this period the duration of an attendance session was determined by the length of the mate's absence. When the mate returned, it often brought a twig for the nest or food for the young. Eggs or young nestlings occasionally were left alone for periods of 5 min or less, and very rarely for as long as 20 min.

The same adult probably sat on the nest every night. I visited a nest on 5 nights and always found the male on the nest. At another nest two visits on different nights found the same bird, of unknown sex, on the nest. In one other case in which the sex of the bird was known, a one-night check found the male brooding the young.

The rate of feeding nestlings is low and shows no daily peak (fig. 6). Each adult visits the nest 0–3 times each hour, from hatching through fledging, with a slight increase as the nestling gets older. For 33 observation sessions of variously aged broods of one, two, or three nestlings, the average rate of feeding by both parents combined was 3.0 feedings/hr. Assuming equal division of the feedings among all nestlings present, each nestling was fed 0.4–4.5 times/hr, averaging 1.8 feedings/nestling/hr. The average for two-nestling broods, 1.3 feedings/nestling/hr (12 observations at 5 different nests), is close to that for single-nestling broods, 1.8 feedings/nestling/hr (10 observations at 4 different nests), both measured during the first 8 days. This low feeding rate is possible because each food item, usually a crushed caterpillar (table 1), is large. Herrick (1910) and Spencer (1943) found similar feeding rates for C. erythropthalmus.

Nest-cleaning behavior was minimal. Egg shells often remained in the nest or were caught on its edge. As is typical for small birds, a sterile egg stayed in a nest throughout the nestling period. I saw no fecal sacs carried away, but Herrick (1910) and Spencer

(1943) reported fecal sacs in young C. erythropthalmus.

Nest defense was similar to that reported for C. erythropthalmus (Spencer 1943) and C. americanus (Hamilton and Hamilton 1965). An incubating bird's first reaction to a potential nest predator, such as a person walking by, was to move quietly off the nest to a different part of the nest tree and preen until the disturbance was past. If the disturbance persisted, the adult was likely to give the disturbance note, a short, quiet cluck or tok. Adults always gave the tok when they arrived with food at the nest and found a person nearby. They sometimes gave a complaining, long mew if the person was disturbing the nest or if a Smooth-billed Ani (Crotophaga ani) was near the nest. Birds further reacted to anis by giving a choked-up, gagging version of the churr, with the mouth wide open. During this vocalization they usually fluffed the feathers, hunched the back, dropped the wings, and fanned the tail. The bird performing this display faced either toward or away from the ani. In an extreme reaction, the cuckoo flew at the intruder and pecked it briefly before continuing the threat display. This display was observed four times against a stuffed ani and three times against live anis, all very close to the nest. The anis, considered to be nest predators, seemed to ignore the threat display, but they did not take eggs from the nests. Other possible nest predators include the Kiskadee Flycatcher (Pitangus sulphuratus), opossums, snakes, and house cats.

DEVELOPMENT OF THE YOUNG

The nestling development of C. pumilus proved to be similar to that previously described for other Coccyzus (Kendeigh 1952). The young left the nest rather early, spending several days in a climbing stage before fledging. In the following schedule of the develop-

ment of *C. pumilus* young, Day 1 is the day of hatching.

Nestling

Days 1, 2.   The skin is dark gray tinted yellowish-green. A scattering of tan, hair-like feathers is on the dorsal tracts. The eyes are closed. Pin feathers are not visible. The mouth lining is bright pink with fine black lines and a pattern of white spots and white bumps with backward-pointing serrations (fig. 5). The nestling lies prostrate on its belly and chin except to lift its head and quiver its wings to beg. It fails to beg at some adult arrivals. Some nestlings can creak this early, but not all do. Through day 5, a nestling may respond to tapping on the nest by begging and creaking.

Day 3.   Small slits open on the eyes. Begging becomes stronger, as it does throughout development. Wing quiver becomes more of a flap.

Day 4.   Some pin feathers show on the wings, tail, and body. The nestling can grasp twigs of the nest with its feet and squawk when picked up. It creaks when begging.

Day 5.   The eyes are partly to mostly open, but begging is not yet directed at the arriving adult. The nestling still lies prostrate, and its head is wobbly. It tries to right itself if laid on its back.

Day 6.   Some feathers erupt from their sheaths, mainly remiges, rectrices, and the abdominal tract. A nestling was seen to stand and defecate over the edge of the nest. Probably even younger chicks defecate in this manner. When the nest is disturbed, the nestling crouches silently in it.

Day 7.   Tufts of pale tan feathers are on the abdomen. The nestling sometimes holds its head up and tries to stand when it begs. The first preening, scratching (directly below the wing), panting, and gular fluttering are observed. One nestling attempted to eat food spilled in the nest.

Days 8, 9.   Feathers on the rest of the body begin to emerge from their sheaths. The nestling is unsteady but may sit on the side of the nest.

Day 10.   The nestling is well feathered, but its plumage is still well sprinkled with bits of feather sheaths. It preens often and hops out of the nest, although unsteadily. Thus begins the climbing stage. The nestling is alert and can see adults at least 20 m away. When disturbed, it hops from the nest. Parents still brood at night and occasionally during the day.

Day 11.   The nestling spends more time out of the nest but is not always steady on its feet.

Day 12.   The nestling is usually out of the nest, preening and hopping hesitantly between perches. It may peck at leaves and pull on twigs. When adults arrive in the nest tree, the young hops toward them. Some young at this age can give the short-*churr* (described below).

Day 13.   Feathers are all out of their sheaths and growing. Tail and wings are about 58% adult length and the bird is about 65% adult weight ($n = 6$ nestlings). The nestling can hop well enough to evade a person, but if pursued, it usually tries to fly and falls to the ground. If it falls out of the tree, it cannot climb back up. It can give the short-*churr* and the threat display.

Days 14–21.   The nestling is mobile in the nest tree and finally "fledges" when it flies to another tree. The exact day of fledging depends on the rate of nestling development and on the distance to the nearest tree.

Fledgling.   The fledgling gradually becomes more mobile and completes feather growth. It passes several days in one clump of bushes or trees, short-*churr*ing frequently, demanding food from the adults when they arrive, and following them in the trees for short distances. The adults probably feed the young less and less, and by 40 days after hatching, the juveniles are almost, if not entirely, independent.

Juvenile.   Juveniles fledged from nests being studied were seen on the study area as long as a month after fledging. One individual 41–49 days old was in the postjuvenal molt, as shown by the rusty feathers scattered on the throat, but it still had the brown eye of a juvenile.

The vocalizations mentioned above need further comment: Young birds when begging often give a "creak," a low, grating continuous *eeeeeee.* This is a soft noise, audible only at close range. It is made by nestlings of all ages and some fledglings. It is probably homologous to what Hamilton and Hamilton (1965) called "buzzing" in *C. americanus*. Few nestlings were handled, but some of those picked up on days 3 to 5 gave a short "squawk." The "short-*churr*" is a soft, short version of the adult *churr*. It is usually only 1–8 syllables long, and sometimes is repeated often, six times a minute. Short-*churr*ing develops at the time the nestling begins to wander away from the nest. This call is probably a location
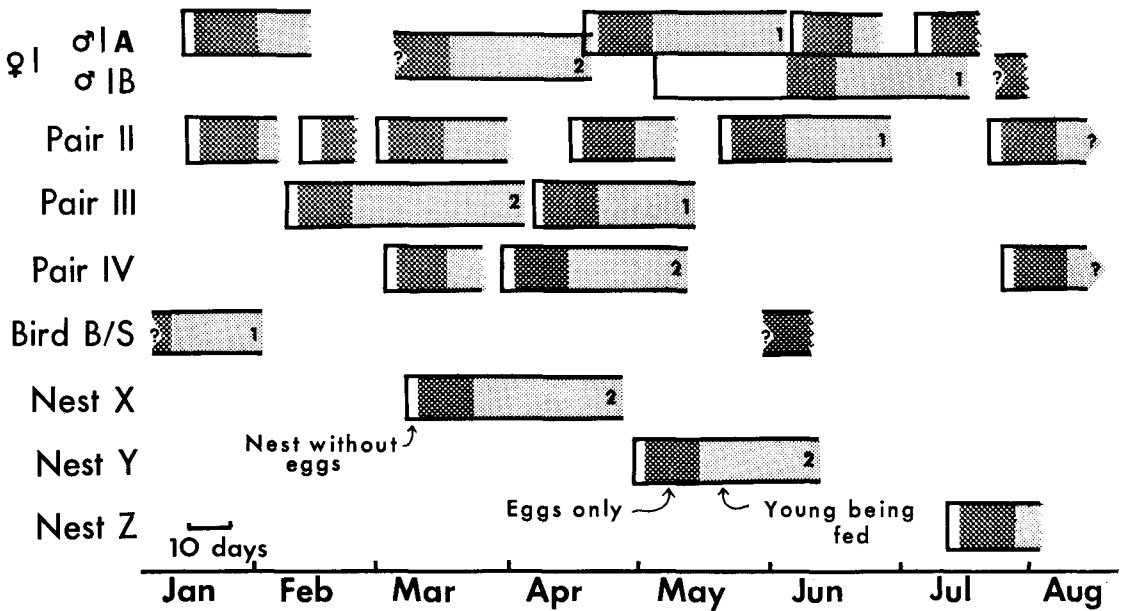
FIGURE 7. Complete nesting activity records of Pairs I to IV and partial records of unmarked pairs on the study area. See text for earlier records of Pair I and an explanation of its relationships in March and April. Nests X and Y may be of the same pair. A ragged endline indicates loss of eggs or young at that date. The number of young fledged is given at the end of the bar. The end of the feeding period is the last day on which adults were seen feeding the fledgling; in most cases feeding probably continued, tapering off, after this. At some nests incomplete data were supplemented with averages from other nests of durations of no-egg, egg, and nestling/fledgling stages.

call given so that the adult can find the young in the dense shrubbery.

The procedure for feeding young includes an unusual behavior. Often an adult freezes in the position of placing the food in the young's mouth. The young and adult may hold this position for 5–125 sec, until they both suddenly relax. The adult withdraws, while the young gulps down the food. Sometimes the adult withdraws the food and begins again by relocating it in the young's mouth. This feeding procedure was observed mostly with nestlings, but occasionally with fledglings. When I placed a caterpillar or the tip of my finger in a begging young's mouth, it closed on the finger or food and held that position. Spencer (1943) discussed this same behavior in *C. erythropthalmus*, as described by several workers.

THE BREEDING CYCLE AND
NONSEASONALITY

Figure 7 summarizes the breeding activity of most birds on the study area over the 7 months January–August 1971. Renesting after a lost clutch is the rule. After a successful brood, a pair may immediately start another nest or may delay awhile. If a second brood is started immediately, the full nesting cycle, from egg-laying to egg-laying, is about 55 days.

Females I and II bred almost continuously during the entire study period, January to August 1971, and were still breeding at the end of this time. Furthermore, previous observations (detailed below) indicate Female I and Male IA nested in August, September, and December 1970. This pair, then, was breeding for an entire year.

For other pairs the 7 months included long non-nesting periods of various durations. Pair IV was not known to have a nest for 74 days after one successful brood. After two successful broods, Pair III did not nest for at least 90 days. Periods of nesting or non-nesting were not synchronized among the various pairs, giving no sign of a population breeding cycle, annual or otherwise. The cues that initiated or terminated breeding in these pairs must be either internal or subtle, possibly very local environmental factors.

Non-breeding periods probably are not required for molt, as they are in many species (Payne 1972), including the Andean Sparrow (*Zonotrichia capensis*) near Cali (Miller 1961). Of two adults caught during nest-building and four adults captured during incubation, all were molting some body feathers, although eight adults caught while feeding young were not. Birds in the field were seen molting rectrices and remiges during all stages of the

TABLE 2. Egg survival, based on 25 clutches, 22 of two eggs and 3 of three eggs, followed to fledging or failure.

Eggs laid[a]	53	
Details of failure		
Infertile	1	
Fell out of nest	1	
Disappeared before other hatched	1	
Disappeared after other hatched	3	
* Whole clutch disappeared	11	
Details unknown	3	
Nestlings hatched	33	62.3% survival of eggs
Details of failure		
One of two disappeared from nest	1	
Dead in nest after other fledged	1	
Trapped by forked branch during climbing stage	1	
* Disappeared in climbing stage	2	
* Whole brood disappeared	4	
Details unknown	1	
Young fledged	23	43.4% survival of eggs 69.7% survival of nestlings

[a] Clutches not discovered until after hatching (7 nests with two, 2 with one nestling) were assumed to have had two eggs. Losses marked * are attributed to predation.

nesting cycle. Also, the flight feathers of any one individual examined in the hand showed all degrees of wear. Smooth-billed Anis in Cuba molt throughout the year, although they are seasonal breeders (Davis 1940).

REPRODUCTIVE SUCCESS

The 43.4% fledging success of eggs (table 2) and the 56.0% success rate of clutches (table 3) are similar to Ricklefs' (1969) averaged values for temperate-zone or arid tropical-zone passerines with open nests. These survival rates are higher than Ricklefs' average for humid tropical species.

I found mortality to be about equal in both the egg and nestling stages. Predation probably takes roughly 32.1% of the eggs and nestlings, accounting for 56.7% of egg and nestling mortality (table 3). This predation rate is in the range of those few reported for temperate-zone species (Ricklefs 1969).

In the 7 months of this study, 23 adult cuckoos using this area of approximately 29 ha pro-

TABLE 3. Success of 25 nests found over the 7-month study period.

	Hatch 2			Hatch 1		Hatch 0
	Fledge 2	Fledge 1	Fledge 0	Fledge 1	Fledge 0	
2-egg clutches[a]	9	1	2	3	4	3
3-egg clutches	0	1	0	0	0	2
Fledged 1 or 2: 14 (56.0%)						

[a] Clutches not discovered until after hatching (7 nests with two, 2 with one nestling) were assumed to have had two eggs.

duced at least 23 fledglings. Of the nine adults carefully followed, none died. With this replacement rate of slightly over one adult per year, the cuckoo population can at least maintain itself, and possibly increase or send out colonizers to new areas.

A CASE OF POLYANDRY

Because males play an active role in all stages of nesting, it is possible for a female to initiate more than one nest. One female consorted with two males simultaneously for at least 5 months, helping one male through three unsuccessful and two successful nests, and the other through two unsuccessful and two successful nests. These two males, IA and IB, frequented many of the same trees, occasionally foraging within sight of each other. They often chased each other from those trees between their nests and from the immediate nest areas. However, this defense was so lax that while the female was incubating or brooding one male's nest, the neighboring male could approach, court, and copulate with her, while the owner male was out of sight. I observed this once for each male.

This trio's history began before the study period. In August 1970, a pair of cuckoos nested in an atypical site, a low, thin lemon tree in a heavily used residential garden. The nest failed, and a pair, presumably the same, was seen building in this same tree in September and again in December 1970. In January 1971, I banded Male IA, who was nesting in this tree, presumably for a fourth time. In March I discovered this bird plus a female and another male feeding three nestlings in an isolated tree about 360 m from the lemon tree nest. The unmarked birds I banded as Female I and Male IB. I believe this female was the same as the previous mate of Male IA, since at dusk one day when the fledglings of this March brood were near independence, I saw her go to the old January nest, sit on it, and *churr*. Of the three nestlings this trio was feeding, two were still in a nest, but the third
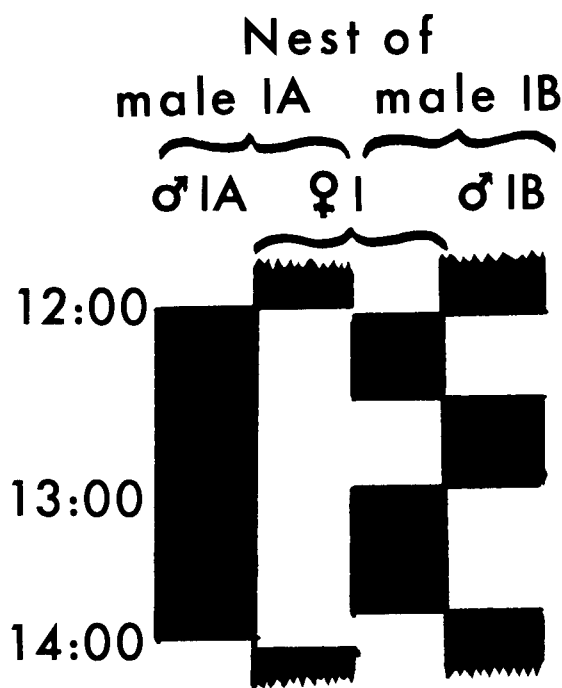
Nest of
male IA   male IB

FIGURE 8. Simultaneous records of incubation sessions at nests of Female I, 15 June, 11:50–14:10. Black bars show the time each bird spent incubating at each nest.

was 4 or 5 days older, already hopping about the tree. This older nestling disappeared 3 days later, presumably fledged, but all three adults continued feeding the two nestlings. Male IB brooded them at night at least once. These nestlings fledged 6 and 13 days after I discovered them. At this nest and at her next nest, each her only clutch at the time, the female brought food as often as her mates. When she laid clutches for both males, so that each had a nest with eggs simultaneously, she helped incubate both clutches (fig. 8). However, when the eggs hatched, although she did feed at both nests, she was lax at one nest. On a morning when the younger of these two broods was 5 days old, the female brought food to this brood only once, while the male did four times. Furthermore, this male, IA, had seemed somewhat confused, bringing 11 twigs to the nest in 2 hr when the 3-day-old nestling was fed only twice. Usually by this stage the parents have ceased, or at least reduced, building activity in favor of brooding or feeding young. This nestling soon disappeared.

This abnormal attendance pattern while Female I was biandrous contrasts with her and Male IA's previously normal parental behavior while monogamous. This suggests that biandrous pairing is an unusual and aberrant

state in this species. Simultaneous polyandry (distinguished from successive polyandry) has been reported in at least one normally monogamous species, the Ovenbird (*Seiurus aurocapillus*) (Hann 1940). This *C. pumilus* female could be another such case of an aberrant individual. On the other hand, I observed this behavior in one out of only four females. It could actually be more widespread in *C. pumilus* than I could discover. Since individuals were very difficult to follow, I observed most behavior at nests. The only way I would have discovered that a female was biandrous would have been to discover both of her nests.

If this biandrous tendency is real, not just an individual's idiosyncracy, it must have some adaptive value, which can be measured in terms of fledging success. The fledging success of this female's eggs while she consorted with two males was only 2/12 (16.7%), compared to the 21/41 (51.2%) fledging success of eggs of monogamous females. Also, this female's nest success while biandrous, 2/5 (40%), compares poorly with the 12/20 (60%) of monogamous females. (Since the samples were small and neither random nor independent, statistical tests on the significance of these differences are inappropriate.) On the other hand, this female in the course of the study period fledged four young, more than any of the three other females. Admittedly, her cost was high. She laid 16 eggs (assuming all eggs in her nests were hers) to produce those young. Female III, the next highest in number fledged, laid only four eggs and produced three young. Still, in these 7 months Female I contributed more to the next generation than did the other three females. To discover the long-term productivity, and thus adaptiveness, of each pairing arrangement, these birds should be followed for many years.

The trio's relationship was interesting also from the male point of view. When both males were feeding the two March nestlings, at least one of them was feeding an offspring of the other. Also, the promiscuity of the female during her biandrous life introduces the possibility that the eggs reared by one male were fertilized by the other. If this is the case, the bonding relationship seems maladaptive for the male. Maynard Smith and Ridpath (1972) discussed this dilemma in the Tasmanian Native Hen (*Tribonyx mortierii*).

Further circumstantial evidence indicated another unusual feature in the *C. pumilus* social system. At a nest with three eggs, three cuckoos were collected, one that was on the nest, one that came to the nest shortly after-

ward, and one, perhaps a neighbor, that came to a nearby tree. All were males. The two that were clearly associated with the nest had testes 6 × 5 mm; the third had testes 8 × 4 mm. Without more information I cannot say if this situation involved a helper at the nest, a communal nest, or some other relationship, but it demonstrates another direction of flexibility in this species' breeding behavior.

DISCUSSION

Comparison of this study with those of North American *Coccyzus* (e.g., Herrick 1910; Bent 1940; Spencer 1943; Hamilton and Hamilton 1965) shows many similarities in behavior, development, and morphology among the members of this genus. These include foraging methods, a fondness for caterpillars, shedding the gizzard lining, a flimsy nest, courtship feeding, the nest defense display, asynchronous development of the young, dark-skinned, almost naked nestlings, long nest attendance sessions and low feeding rates, nestling creaking, and the behavior of freezing in position while feeding a nestling. Many of these characters are also shared with other Cuculidae, even those in other subfamilies (Kendeigh 1952; Austin and Singer 1961; Skutch 1966).

Comparisons between tropical- and temperate-zone bird species (Ricklefs 1968) show that, on the average, tropical species have smaller clutches, longer breeding seasons, lower nest success, slightly longer incubation periods, very slightly longer nestling periods, longer fledgling dependency, and longer intervals between nest attempts. As we have seen, *C. pumilus* has the "typically tropical" extended breeding season, but, when compared to temperate-zone passerines, *C. pumilus* has equally good, rather than lower, nest success. Data are also available to compare clutch size and development rates. Bent (1940) reported that *C. erythropthalmus* often lays two or three eggs, occasionally four or five. *C. americanus* usually lays three or four, but may lay one or five. In both species clutches of more eggs than this are probably the work of more than one female. This study found that *C. pumilus* usually lays only two, occasionally three, eggs although a female is capable of laying more. In clutch size, then, *C. pumilus* fits the tropical pattern. Turning to egg and nestling development rate, the incubation periods of the North American species have been reported as 14 days (Bent 1940), 10–11 days (Spencer 1943), and 10–11 days (Hamilton and Hamilton 1965). As Hamilton and Hamilton (1965) explained, the figure in

Bent is doubtful. *C. pumilus* requires a longer incubation, 13 days. The North American species leave the nest at ages 7–9 days (Bent 1940), 6–7 days (Spencer 1945), and 8 days (Hamilton and Hamilton 1965). *C. pumilus* leaves at about 9 days of age (on day 10 in the above schedule), at the upper limit of the range found in the North American species. Thus in these aspects of development, *C. pumilus* supports the generalizations about tropical species.

Of special interest are any social or reproductive habits that could elucidate the evolution of the unusual breeding systems of other Cuculidae. These other breeding systems include brood parasitism by many Old World and some New World cuckoos; nest sharing, helpers at the nest, and perhaps polygamy in *Crotophaga*, the New World anis (Davis 1940; Skutch 1959, 1966; Köster 1971); and in the Black Coucal (*Centropus grillii*) polyandrous females that do not help care for eggs or young (Vernon 1971). Certain characteristics of the genus *Coccyzus*, especially demonstrated by *C. pumilus*, are expressions of these familial tendencies, but have not evolved to the extreme conditions found in these other groups. Hamilton and Orians (1965) considered the short incubation period, the wide food tolerances of nestlings, and the careful searching behavior of cuckoos as preadaptations of this family to brood parasitism. I will consider four additional characteristics of the genus *Coccyzus* that express the family potential for a variety of breeding systems, including brood parasitism.

1. Participation by the male in nest building, incubation, and feeding nestlings at least partly emancipates the female, leaving her time to consort with other males or discover other nests in which to lay. In *C. pumilus* the male carries at least half the load of nesting duties, and in two cases was known to incubate or brood at night. In other *Coccyzus* and more distantly related cuckoos, males also help in nesting. For example, in both Groove-billed and Smooth-billed Anis (*Crotophaga sulcirostris* and *C. ani*), Skutch (1959, 1966) found males on the nests at night.

2. Kendeigh (1952), following Herrick (1910), suggested that a characteristic of the Cuculidae was the uncoupling of egg-laying from the "normal" nesting sequence of courtship, nest-building, egg-laying, incubation, and care of young. This uncoupling is manifested as egg-laying at irregular intervals of 1–3 days. In *C. pumilus* and probably *C. erythropthalmus* (Spencer 1943), egg-laying occurs before nest construction is complete.

More interesting in terms of the development of brood parasitism or communal nesting is that these species also lay eggs in irregular places. *C. americanus* and *C. erythropthalmus* occasionally lay in nests of non-cuckoos, in nests of each other, or in nests of other females of the same species (Bent 1940). As discussed above, *C. pumilus* may do the same.

3. The nature of the territories of the North American cuckoos is not known in the literature. For *C. americanus*, Hamilton and Hamilton (1965) found a large home range, but they saw no clear evidence of territoriality. Since the North American *Coccyzus* often exploit abundant and concentrated food sources, as does *C. pumilus*, I would predict they have common feeding areas as does *C. pumilus* in Cali. Besides sharing feeding areas, *C. pumilus* does not defend its nest territory effectively. Both of these behaviors permit members of neighboring pairs to come into contact, with the possibility of developing multiple pair bonds.

4. An opportunistic breeding physiology is suggested in North American cuckoos since they appear in greater numbers where tent caterpillars are abundant and since they are known to nest very late in the season (Hamilton and Hamilton 1965). Observations of *C. pumilus* indicate it is ready to breed at any time: the pair bond is maintained all year, courtship feeding occurs at all times during the nesting cycle, and molt may not require an exclusive, nonbreeding period. Where the climate is equitable all year, as it is some years in the Cauca Valley, *C. pumilus* will breed year-round. A pair may repeat nesting attempts all year, and some birds in the population will be nesting at any time during the year. A constant readiness to breed or a rapid response to stimuli to breed would facilitate evolution of a response to other individuals nesting and thus the evolution of brood parasitism or communal nesting.

This study dealt with a peripheral population of *C. pumilus* during a year of short or modest fluctuations of rainfall. In other parts of its range and in other years in Cali, *C. pumilus* faces distinct seasons of drought and rainfall. Under this other regime its breeding system might be more like that of the temperate-zone species, with a shorter, synchronized breeding season and a larger clutch size. This might be where the advertisement song, which Schwartz recorded in Venezuela, is used, if attracting a mate is a periodical problem. Also, if the dispersion of food is appropriate, home ranges may be more territorial. The relaxed territorial defense and the ten-dency to polyandry seen in Cali may be facultative traits expressed only in the conditions found there. They also could be genetically fixed traits found only in this peripheral population. In either case, the flexibility within this species could account in part for the success of the Dwarf Cuckoo in colonizing new territory in Colombia.

SUMMARY

A population of the Dwarf Cuckoo was studied in the tropical pasture land around Cali, Colombia, near the edge of its range. Four color-marked females and their mates were followed closely for 7 months. Throughout this period the weather in Cali was warm and moist.

Two females bred almost continuously throughout this period, and one was probably breeding for an entire year. The other two females had long nonbreeding periods, not synchronized with each other. The members of all pairs remained together throughout the study. Courtship feeding occurred at all stages of the nesting cycle and between nestings.

Home ranges of pairs are large and widely overlapping. A small area around the nest is defended, but not effectively. I heard no true song, although Schwartz has recorded a song in Venezuela.

Both sexes help build the nest, incubate the eggs, and brood and feed the young. The clutch of two or three eggs is laid while the nest is very scanty, so construction continues through incubation. Incubation begins with the first egg and takes about 13 days. The nestling leaves the nest on about day 10 but stays in the nest tree until day 14 or later, when it first flies to another tree. Nestling food is almost entirely caterpillars.

As might be expected of a tropical species, the clutch of *C. pumilus* is smaller than those of the temperate-zone *C. erythropthalmus* and *C. americanus*, and the development rate is slightly slower. However, nestling morphology and behavior, adult defense displays, and other aspects of nesting behavior are similar to those of these North American species.

Of 53 eggs in 25 clutches, the survival to fledging was 43.4%. Predation probably accounted for 56.7% of egg and nestling mortality. Nest success was 56.0%.

Certain characteristics of *C. pumilus* and of other *Coccyzus* are considered as modest expressions of the potential in the Cuculidae for unusual breeding systems. The tendency toward unusual breeding systems and a flexibility within the species are exemplified by one

female who was polyandrous, nesting with two males simultaneously.

ACKNOWLEDGMENTS

LITERATURE CITED

AUSTIN, O. L., JR., AND A. SINGER. 1961. Birds of the world. Golden Press, New York. 316 p.

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. Bull. U.S. Natl. Mus. 176.

BORRERO, J. I. 1946. Aves ocasionales en la sabana de Bogotá. Caldasia 4:169–173.

CRIST, R. E. 1952. The Cauca Valley Colombia. Land tenure and land use. Waverly Press, Baltimore, Md. 118 p.

DAVIS, D. E. 1940. Social nesting habits of the Smooth-billed Ani. Auk 57:179–218.

ESPINAL T., L. S., AND E. MONTENEGRO M. 1963. Formaciones vegetales de Colombia. República de Colombia, Instituto Geográfico "Agustín Codazzi," Departamento Agrológico, Bogotá. 201 p.

FORBUSH, E. H. 1927. Birds of Massachussetts and other New England states. Part II. Land birds from Bob-whites to Grackles. Norwood Press, Norwood, Mass. 461 p.

HAMILTON, W. J., III, AND M. E. HAMILTON. 1965. Breeding characteristics of Yellow-billed Cuckoos in Arizona. Proc. Calif. Acad. Sci. (ser. 4) 32:405–432.

HAMILTON, W. J., III, AND G. H. ORIANS. 1965. Evolution of brood parasitism in altricial birds. Condor 67:361–382.

HANN, H. W. 1940. Polyandry in the oven-bird. Wilson Bull. 52:69–72.

HERRICK, F. H. 1910. Life and behavior of the cuckoo. J. Exp. Zool. 9:169–233.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22:1–356.

KÖSTER, F. 1971. Zum Nistverhalten des Ani, Crotophaga ani. Bonn. Zool. Beitr. 22:4–27.

LEHMANN, F. C. 1957. Contribuciones al estudio de la fauna de Colombia XII. Novedades Colombianas, Museo de Historia Natural, Universidad del Cauca, Popayán 1:101–156.

MAYNARD SMITH, J., AND M. G. RIDPATH. 1972. Wife sharing in the Tasmanian native hen, Tribonyx mortierii: a case of kin selection? Amer. Nat. 106:447–452.

MCATEE, W. L. 1917. Shedding of the stomach lining by birds, particularly as exemplified by the Anatidae. Auk 34:415–421.

MEYER DE SCHAUENSEE, R. 1964. The birds of Colombia. Livingston, Narberth, Pa. 426 p.

MILLER, A. H. 1961. Molt cycles in equatorial Andean Sparrows. Condor 63:143–161.

NICÉFORO MARIA, HNO, AND A. OLIVARES, O. F. M. 1966. Adiciones a la avifauna colombiana. III. (Columbidae-Caprimulgidae). Bol. Soc. Venez. Cienc. Nat. 26:370–393.

PAYNE, R. B. 1972. Mechanisms and control of molt, p. 103–155. In D. S. Farner and J. R. King [eds.], Avian biology, Vol. II. Academic Press, New York.

RALPH, C. P., AND S. J. CHAPLIN. 1973. Some birds of Isla Punta Arenas, Pacific Coast, Colombia. Condor 75:357–359.

RICKLEFS, R. E. 1968. The nesting cycle of songbirds in tropical and temperate regions. Living Bird 8:165–175.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. No. 9. 48 p.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

SKUTCH, A. F. 1959. Life history of the Groove-billed Ani (Crotophaga sulcirostris). Auk 76: 281–317.

SKUTCH, A. F. 1966. Life history notes on three tropical American cuckoos. Wilson Bull. 78:139–163.

SPENCER, O. R. 1943. Nesting habits of the Black-billed Cuckoo. Wilson Bull. 55:11–22.

VERNON, C. J. 1971. Notes on the biology of the Black Coucal. Ostrich 42:242–258.