

THE PLAIN-FRONTED THORNBIRD: NEST CONSTRUCTION, MATERIAL CHOICE, AND NEST DEFENSE BEHAVIOR

BETSY TRENT THOMAS

Some members of the Furnariidae construct elaborate enclosed nests (Hudson 1920, Skutch 1969a); one of the largest nests is that made by the Plain-fronted Thornbird (*Phacellodomus rufifrons*). Short (1975) gives a map of the range of the *Phacellodomus* superspecies complex showing two disjunct populations, while Vaurie (1980) shows a map with three disjunct populations. Meyer de Schauensee and Phelps (1978) coined the name Plain-fronted Thornbird for the northern race *P. r. inornata* because, even in hand, the rufous front of this race is not well-marked. Skutch (1969b, Pts. 1, 2) has given a life history account of the bird in Venezuela. However, his observations were limited to unbanded birds in 5 months of a single season. Herein I confirm and supplement many of Skutch's (1969b) conclusions and give additional information about the nest, its construction, nest piracy, and attempted nest predation based on 3 and 4 years of observations of banded pairs and their young.

STUDY AREAS AND METHODS

I watched thornbirds at two different Venezuelan sites. One banded pair and their young were followed for 4 years in a scrub and grassland area 30 km south of Caracas at Los Anaucos, Estado Miranda (elev. 550 m). Another banded pair at the same site was observed for less than a year. In the Venezuelan llanos, a savanna, at Fundo Pecuario Masaguaral (Thomas 1979), in Estado Guarico (elev. 63 m) I watched banded territorial birds for 3 years and others for shorter periods. Observations of other thornbirds were also made in both study areas at a number of nests where only one bird or none was marked. The birds were mist-netted and marked by placing plastic color-bands on their legs.

RESULTS

The sexes.—Plain-fronted Thornbirds are monomorphic. Both members of a pair share in all phases of the reproductive cycle, thus the sexes are difficult to distinguish in the field. With prolonged observations of banded pairs, however, I found that one of them did more, or in one case most, of the diurnal incubating and brooding. It was this same bird of each pair that twittered more often in response to its mate's loud calls, although both are capable of loud calling. I therefore agree with Skutch (1969b) that this bird is probably the female. In the pair which I watched for 4 years I saw one nuptial feeding which further confirmed this assessment of the sexes.

Nests and nest-building.—In the tropical countryside of northern Venezuela one is seldom far from the sight of a thornbird nest. These conspicuous structures are from 0.5–2 m ($N = 20$) long and the main body has a fairly uniform diameter of 40 cm, not including sticks extending out irregularly from it. Nests are generally suspended from the outer branches of large, isolated trees or on the open side of trees at the edge of deciduous woodlands. Some trees support as many as five nests, or parts of nests, yet in no instance did I ever find more than a single pair of thornbirds and their young occupying a nest tree and its adjacent territory. In color-banded birds of known relationship the extra birds have been the offspring of the territorial pair. Unbanded birds whose relationship to the territorial pair was unknown were occasionally found in the territory.

Thornbirds readily build new nests at any time of year when an occupied nest falls down or when the bottom end, site of the preferred sleeping and breeding chamber, has been usurped by other species of birds. Thus, trees contain old nests and the current nest of the same pair. Vaurie (1980) questioned whether thornbirds use the same nest in succeeding breeding seasons; definitely they do. The thornbird nest is used all year for roosting and I observed three nests 11–13 months after one breeding season in which eggs of the next season were laid. In this respect *P. ruffrons* differs from several other common Furnariidae, such as Pale-breasted (*Synallaxis albescens*) and Yellow-throated (*Certhiaxis cinnamomea*) spinetails, which also build elaborate stick nests but only for one season's breeding and not for roosting.

Throughout the year thornbirds add to their nests and rearrange sticks on them. When they build a new nest they do most of the work in the early morning hours, with the work gradually diminishing by about 09:30. Occasionally, they build at mid-day and again in late afternoon. When one nest fell during the breeding season it was replaced and eggs laid in less than 3 weeks.

Just prior to egg-laying the pair spends much of the morning vocalizing at the nest. If they are not breeding and the nest is not being used by other species, thornbirds often leave their nest at dawn and do not return until dusk.

The longest thornbird nests are in the llanos ($\bar{x} = 82.3$ cm, $N = 10$), whereas in the tropical areas of the Venezuelan coastal mountains, thornbird nests are shorter ($\bar{x} = 51.5$ cm, $N = 10$). I believe the difference may be related to the abundance of the Troupial (*Icterus icterus*) in the llanos (in contrast to the much smaller numbers of Troupials at higher elevations) because there thornbirds keep adding additional sticks to the tops of Troupial-pirated nests. Unfortunately, this hypothesis is not easily tested as there is no broad area in Venezuela where the thornbird lives in the ab-

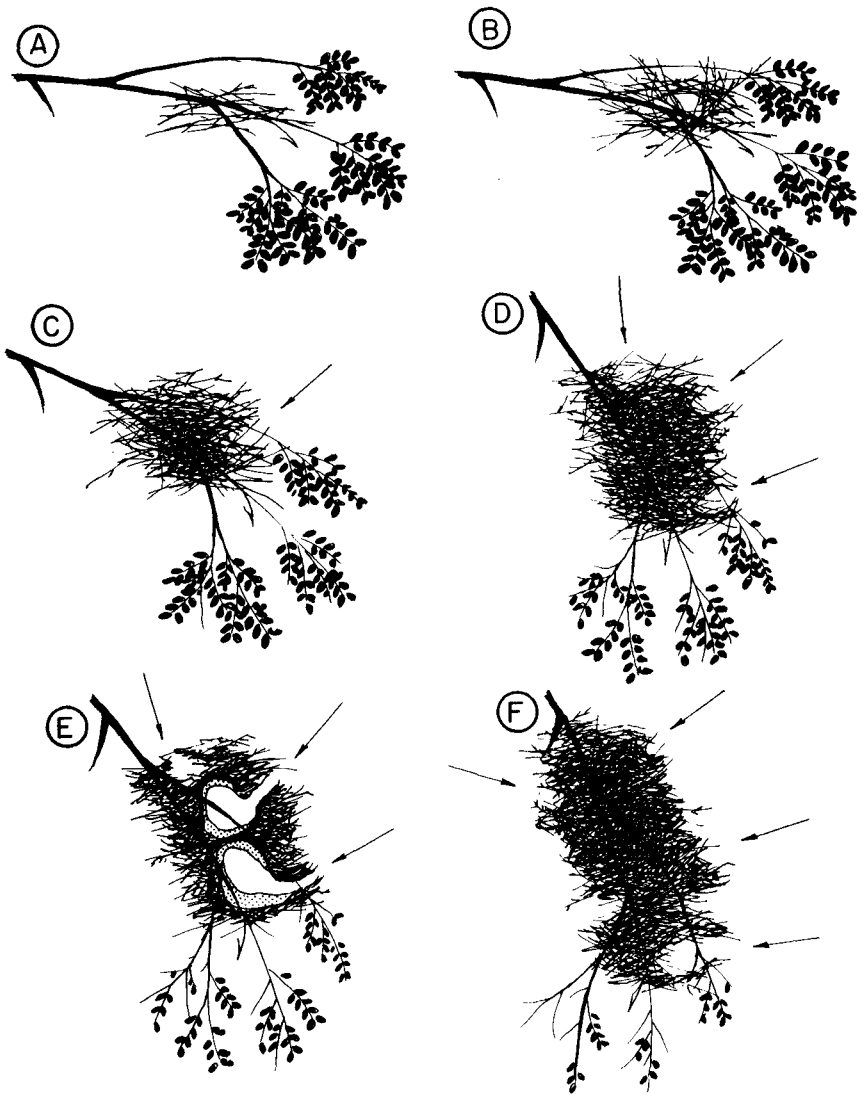


FIG. 1. Plain-fronted Thornbird nest showing successive stages of construction. In cross section E the nest lining is indicated by dotted areas. Arrows indicate entrances to nest chambers.

sence of Troupials, although the reverse is true: Troupials live where there are no thornbirds (Phelps and Phelps 1963).

Thornbird pairs choose their nest-site with much twittering and inspection. On four occasions I observed pairs repeatedly showing interest in certain tree branches even though they already had built a substantial nest. Later, those same branches were used for a replacement nest. After the selection of a site, both members of the pair carry sticks to a place on the chosen branch where there is a forked intersection. Usually the first sticks fall down, or a few may catch, but often wind demolishes the first fragile platform. One pair worked 5 days before their first sticks stayed in place overnight (Fig. 1A). As soon as a platform is established, the birds begin building up the sides to form a steep, conical cup roughly 30 cm across the top and 15 cm deep inside (Fig. 1B). As the cup deepens sticks are laid horizontally across the rim and gradually the center is roofed over as in Fig. 1C. At this stage the birds begin roosting inside and probably also begin to line this first chamber. Even pairs without young continue to build, adding more sticks to the top of the nest to form a second cup, which is roofed over as before. Many thornbird nests have four or more chambers stacked one on top of the other, each with its own entrance, and not interconnected with the others (Fig. 1D,E). Often the upper chambers, which are sometimes lined, are reached through entrances which protrude slightly, like pockets (Fig. 1F). As Skutch (1969b) reported, there is usually an antechamber, or tunnel, leading into each chamber. Most nests are built on outer tree branches which may be bent downward through an arc of 60° or more as the weight of the nest increases. The basic shape of the first conical nest cup, now rotated as in Fig. 1E, can be seen where the back and bottom, including the entrance tunnel, of the lowest chamber preserve the original cup shape.

When the much larger Troupial attacks a nest, it enlarges the lowest chamber by pulling out sticks and nest material to get inside. The thornbird's response is to roost in an upper chamber and to build more chambers on the top of the nest, or to abandon the nest entirely and start a new one. Thornbird nests appear to be very compact, but a flashlight inserted into one at night reveals hundreds of holes. Thus, the nest is probably well ventilated, and the interstices allow the birds inside to see out. This may explain a bird's rapid flight from the nest when a predator approaches (Skutch 1969b, pers. obs.).

Nest materials.—The sticks of nests are so tightly interlaced that a fallen nest can be picked up nearly intact by the stub of the broken branch. I took apart a fallen thornbird nest at Los Anaucos in August 1978. The nest contained three eggs, only one of which was smashed in the well-

TABLE 1
STICKS FOUND IN A LOS ANAUCOS NEST OF THE PLAIN-FRONTED THORNBIRD

Length (cm)	Thorny sticks	Non-thorny sticks
1-10	325	1268
10-20	262	966
20-30	79	202
30-40	22	41
>40	10	7
Total	698	2484

lined chamber by the 5 m fall. The nest measured 56 cm in length and 43 cm in diameter and was typical of smaller nests. A pair and two of its young from the previous year had been using it. There were two nest chambers but, as usual, the eggs were in the bottom one, which had an inside diameter of about 12 cm. The nest lining was thinner on the top (2-4 cm) and thicker on the bottom (4-5 cm), as in Fig. 1E.

While taking the nest apart I was careful not to break any of the sticks, which I sorted into five classes by length: 1-10, 10-20, 20-30, 30-40, and over 40 cm; a few sticks less than 1 cm long were not counted. All the sticks were between 1-5 mm in diameter. Each size class was also divided into thorny and non-thorny sticks. A thorny stick was one with thorns sharp enough to pierce my finger easily (Table 1). I separated the breeding chamber lining from the nest structure but did not count the dry grasses which made up its bulk because, after a year as the nightly roost for 2-5 birds, much of the floor had been ground to a fine powder.

Other materials used in both the nest and the lining were of two kinds—natural and man-made. The natural materials were: one dry rolled seed pod, one butterfly wing, two other insect wings, 11 dry bamboo leaves, 13 miscellaneous dry leaves, 19 pieces of roots, 39 thin, papery pieces of bark, and 97 pieces of tree bark. Man-made components included a small piece of paper, a piece of window screening about 5 cm², and more than 160 fragments of thin plastic, each greater than 1 cm². The plastic pieces had not been placed indiscriminately; they generally formed a layer between the sticks of the outer nest and the grass nest-lining.

I found that there were nearly four times as many non-thorny sticks as thorny ones in the nest and that almost twice as many sticks, by weight, were in the 10-20 cm class. The longest thorny and non-thorny sticks were 46.7 and 52.4 cm, respectively. Many of the thorny sticks had 2-4 cm thorns at regular intervals. Intuitively it would seem as though thorny sticks should be more desirable for constructing the tightly linked nest.

TABLE 2
STICK CHOICE EXPERIMENTS

Test 1. Four trays with five matching sticks of each category, total stick-hours of each type offered, 300; Los Anaucos 15 h on 4 days combined.

	Thorny (10–20 cm)	Non-thorny (10–20 cm)
Sticks taken	41	24

Test 2. Four trays each with five matching sticks of two size-classes all non-thorny, total stick-hours of each size offered, 80; Los Anaucos 4 h on 2 days combined.

	Short (10 cm)	Long (20–30 cm)
Sticks taken	19	15

Test 3. Four trays each with 12 matched sticks, two sticks of each size and of each type, total stick-hours for each size and type, 160; Los Anaucos 20 h on 8 days combined.

	Thorny			Non-thorny		
Length in cm	10	20	30	10	20	30
Sticks taken	15	30	36	4	12	6

Test 4. One tray with 12 matched sticks as in test 3, total stick-hours for each size and type, 52; Masagual 26 h on 6 days combined.

	9	7	7	2	1	0
Sticks taken						

However, Skutch (1969b) also found that the birds he observed used predominantly non-thorny sticks, and he questioned the justification of the birds' common name. Were non-thorny sticks preferred by thornbirds, or did this use reflect their abundance in the environment?

Experiments.—When thornbirds build new nests, they transfer sticks from their old nests, whether the nests are still hanging on the tree or fallen below it. Birds even remove sticks from nests still in use for nightly roosting. A series of tests was made to find out the size and type of sticks birds would select when offered carefully matched pairs of sticks of the size (diameter and length) and type (thorny and non-thorny) used in nest-building. I cut dry thorny and non-thorny sticks to experimental lengths from plant species available in territories of the birds. These sticks were placed in identical trays on the ground near a pair building a new nest. Only one kind of test was made on each day, and most tests were made in the first 3 h of the day. At the end of each hour I replaced sticks that were taken, thus beginning a new test each hour. I combined test results as there was no evidence that choice differed with the hour or the nest-building stage (Table 2).

I watched the birds make selections which appeared to be a matter of choice. Once a bird found a tray, its mate quickly followed. Both birds

flew from their nest directly to the edge of the tray or landed beside it. A bird paused, looked at the sticks, then hopped up to and picked up a stick at the mid-point with its bill. Occasionally a bird discarded the first stick chosen and selected a different one instead. Then the bird flew with the stick back to its nest, often flying to successively higher branches as described by Skutch (1969b). As most tests were made with the same pair of Los Anaucos birds, I also tested a pair of birds at Masaguaral. Although I have fewer data from the latter, the results are essentially the same.

When offered a choice thornbirds selected more thorny than non-thorny, and generally longer than shorter sticks. Therefore, it might be that sticks of preferred attributes are limited in the habitats that I studied. Collias (1964) suggested that thorns deter predators as Skutch (1969b) and I both learned when we tried unsuccessfully to insert our hands into nest chambers.

Contributions to nest building by 'helpers.'—The morning after a wind storm destroyed the bottom half of a Los Anaucos nest, the principal pair began to construct a new nest on the same branch, but at a fork below the part of the nest still intact. That night the adults and their three young (about four months old) spent the night in the upper section. (Young spent up to 16 months roosting in the nest.) Each day the pair spent much of the morning working on and calling from the new nest. They transported most of the sticks from the upper section to the new nest and by the sixth night all five birds roosted in the new nest. During 354 min of observation on five different days the male brought 112 (53.6%) of the sticks, the female 69 (33.0%) and two of the three young helped by bringing 17 (8.1%). However, the young birds primarily contributed 2–4 cm pieces of nest-lining. Eleven (5.3%) sticks were brought by unidentified birds.

What happens to nests?—In 57 months the Los Anaucos pair built 12 complete nests and laid small foundations for four others that were never completed. The events which made replacement nests necessary were: (1) six times the nest-supporting branch broke off; (2) once wind tore out the bottom half of a nest; (3) twice the entire half of a nest tree collapsed; and (4) twice the nest was abandoned (once after predation and once because of Troupial interference). However, this pair fledged eight young in four breeding seasons. At Masaguaral, where the Troupial is especially abundant, nests were more often lost because of piracy by this icterine. In 45 months in one territory six nests were built: five were lost to Troupials and one to wind. One other nest was started but not completed.

Interactions with Troupials.—Skutch (1969b) outlined the manner in which a Troupial takes over the lower, principal chamber of the nest. At Masaguaral several times I found two Troupials roosting in a single thorn-

bird nest, but in separate holes. They use nests for breeding and also roost in them all year.

Troupials are not secretive about their piracy. They call near a nest and often begin take-over by vigorously pulling out sticks. One bird at Masagual tore at a nest and dropped the sticks on the ground below. If a stick it pulled out caught in the bottom of the nest the Troupial removed it again, even leaning far over backwards to make sure the stick fell to the ground. In 15 min the bird removed 47 sticks, tearing out about six sticks at a time, which were dropped directly below the nest, and then carrying the next stick 2–6 m away from the nest. Sightings that are occasionally reported of Troupials carrying sticks may be a result of this type of behavior rather than nest construction. Commonly, when a Troupial takes over the bottom chamber of a thornbird nest, it also removes some sticks from above that chamber which gives the nest a profile resembling a narrow-waisted wasp (Fig. 1F). At this point the nest sometimes gradually separates and occasionally thornbirds breed in the bottom part of the upper section as though it was totally independent of the rest of the nest.

Skutch (1969b) made no mention of nest defense by thornbirds, but I saw thornbirds (\bar{x} weight = 24 g, N = 31; see Thomas 1982) defend nests against Troupials (\bar{x} weight = 68 g, N = 4; see Thomas 1982) on a number of occasions. On the morning of 5 July 1978, a Troupial, although rare in the area, found the Los Anaucos study nest and called from the top of the nest tree. It returned in the late afternoon of the same day and began tearing out sticks from the bottom. The thornbird pair was very excited, calling and hopping about on the top and back side of their nest; their vocalizations attracted one of their 10.5 month-old young. Then the Troupial froze motionless for 9 min, its feathers tightly sleeked, while clinging to the entrance of the lower chamber of the nest. Finally, at 19:05, the Troupial forced its way inside. Ten min later the thornbirds went quietly to roost in an upper chamber of the nest.

The following day the Troupial called, often from near the nest. However, that evening the thornbird pair and their two yearlings entered the remodeled lower chamber before the Troupial. Four min later the Troupial entered the same hole causing three of the four thornbirds to fly out in alarm, but the male thornbird remained, clinging upside down to some sticks below the entrance hole. The Troupial perched above it in the enlarged entrance and jabbed its bill down into the thornbird's abdomen. The thornbird lost a number of feathers before it flew away. After that the Troupial pulled out more nest material and then moved inside. Then the male thornbird returned to the lower chamber entrance and, joined by another thornbird, twittered excitedly. This thornbird suffered no permanent injury.

At Masaguaral two Troupials had been roosting nightly, for more than a month, in the bottoms of two adjacent thornbird nests. The thornbirds were building on the top of the newer nest, taking sticks from the older one 1 m distant. On 23 May 1980 I watched the banded female of the pair while she added sticks to the top of the nest. A stick dropped and she darted down after it over the side of her meter-long nest, but stopped at the large Troupial hole at the bottom, which she entered. Instantly a Troupial, which I had not previously noticed, flew in after her. The thornbird uttered a distress "scream," unlike any call I had ever heard from a thornbird. The sound quickly attracted birds of six species to the vicinity of the nest, including a second Troupial which also flew into the same hole. At this point the thornbird flew out, pursued by a Troupial. This thornbird was not seen again. Five days later its mate appeared to be mated with an unbanded individual.

Parasitism.—Skutch (1969b) cited a report that thornbird nests are parasitized by Striped Cuckoos (*Tapera naevia*). On 30 September 1977, at Masaguaral, I found a large, loudly begging fledgling Striped Cuckoo being attended and fed by a pair of thornbirds. The cuckoo was about 2.5 times the size of its foster parents.

Nest predation.—Nestling thornbirds are extremely vocal, behavior unusual for tropical nestlings, which may make them obvious to predators. At a Masaguaral nest I observed a predation attempt. Tropical nest predation is common (Ricklefs 1969) but because it is seldom observed, I have included the following account of the birds' behavior paraphrased from my field notes. On 12 August 1981, I was watching a thornbird nest at which the banded adults were feeding noisy nestlings:

- 17:35—A Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) flew from a wooded area to a tree about 15 m from the thornbird nest, landing at nearly the same height as the nest, and perched motionless in the crotch of an upright branch.
- 17:36—The female thornbird returned to the nest with food in her bill, but she paused momentarily on the nest before going to the nest hole to feed her begging young. She saw the owl and instantly dropped the food she was carrying and flew toward the owl uttering a chipping call. As she reached a branch 7 m from the owl, she was joined by the male thornbird, who also chipped. They faced the owl and moving to within 2 m of it, they continued to call. A Rusty-margined Flycatcher (*Myiozetetes cayannensis*), attracted by the thornbird chipping, flew to a nearby branch and called; other birds gathered overhead.

- 17:40—The owl flew back into the woods with several birds, including the thornbirds, in pursuit.
- 17:52—The female thornbird returned to the nest and fed the nestlings.
- 18:13—Chipping heard again.
- 18:14—The owl returned to the same tree as before but perched on a different branch, 2 m closer to the thornbird nest. The female thornbird chipped from about 4 m above the owl. Abruptly she stopped and darted into the nest hole with her nestlings. The male thornbird also returned to the nest and quickly entered the same hole.
- 18:16—The thornbirds were silent.
- 18:19—The owl flew to a branch of the nest tree and then onto the nest. Twice it went into an empty hole near the top of the nest. Then it perched on a branch 2 m away and looked (probably listened) toward the nest.
- 18:20—The owl flew back to the nest and directly to the correct (lower) nest hole, which was visually less conspicuous than the first hole it had tried. The owl went into the nest tunnel several times. It was far enough inside that only the end of its tail was visible, but each time it withdrew, apparently because it was repulsed by the adult thornbirds within. No sound was audible from where I sat at 20 m distance.
- 18:22—The owl then flew to a different branch in the nest tree, slightly below the level of the nest hole and about 2.5 m away and faced the nest.
- 18:31—An unbanded thornbird which had been roosting each night in a third hole, on the upper side of the nest, flew directly and silently to its hole, as it had done on the previous night. From the direction the thornbird came, it may well have been unaware of the waiting owl.
- 18:46—The owl turned away from the thornbird nest and flew into the woods.
- 18:50—A second unbanded thornbird came to roost, cheeping noisily, pausing as it had on the previous night in a bush directly below where the owl had last perched. Then it flew, still cheeping, to join the other unbanded thornbird for the night.

CONCLUDING REMARKS

Using the nest that I took apart as a measure, I estimated that a 2 m-long nest contains approximately 11,384 sticks and has a probable dry

weight of about 7.22 kg, or 300 times heavier than the weight of the birds that built it.

Thornbird nests appear to be energetically expensive. Nest-building and care is done mostly by the territorial pair with the male apparently being the principal builder. The young, which roost in the nest up to 16 months of age, occasionally bring nest-lining material and a few sticks. Young do adjust sticks on the exterior of the nest but their contribution to building and maintenance is minimal.

One possible advantage of thornbird sociality might be defense of the territory by the young against conspecifics, particularly when the principals are occupied with the long breeding sequence (incubation 16–17 days, nestling period 21–22 days [Skutch 1969b]). During territorial disputes as many as seven thornbirds gather and call defensively. In my observation of one Troupial attack, a young bird did join its parents in nest defense, but no other thornbirds responded to the predation attempt by the pygmy-owl.

SUMMARY

Pairs of Plain-fronted Thornbirds (*Phacellodomus rufifrons*) maintain permanent territories and construct elaborate stick nests for breeding and for roosting throughout the year. Nest material was examined and measurements were made of the size and type of sticks used in one nest. Experiments showed that thornbirds, when given a choice, preferred long, thorny sticks, even though long, thorny sticks were not in the majority by either number or weight in the nest examined. The method of nest construction is described. Thornbird young continue to roost in the nest up to 16 months of age, and they occasionally bring sticks and lining material, but their contribution to nest-building and maintenance is minimal. Nest piracy by the Troupial (*Icterus icterus*) is described as is an apparent nest predation attempt by the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*).

ACKNOWLEDGMENTS

I thank R. Haven Wiley for valuable suggestions on an early draft of this paper, reviewers John O'Neill and John Weske for their help, and Tomás Blohm for sustained hospitality at Masaguaral.

LITERATURE CITED

- COLLIAS, N. E. 1964. The evolution of nests and nest-building in birds. *Am. Zool.* 4:175–190.
- HUDSON, W. H. 1920. *Birds of La Plata*. J. M. Dent and Sons, Ltd., London, England.
- MEYER DE SCHAUENSEE, R. AND W. H. PHELPS, JR. 1978. *A guide to the birds of Venezuela*. Princeton Univ. Press, Princeton, New Jersey.
- PHELPS, W. H. AND W. H. PHELPS, JR. 1963. Lista de las aves de Venezuela con su distribución. Tomo I, Pte. II, Passeriformes (2nd ed.). *Bol. Soc. Ven. Ciencias Nat.*, 24, Nos. 104, 105. Caracas, Venezuela.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. to Zool.* No. 9.

- SHORT, L. L. 1975. A zoogeographic analysis of the South American Chaco avifauna. *Bull. Am. Mus. Nat. Hist.* Vol. 154:Article 3.
- SKUTCH, A. F. 1969a. Life histories of Central American birds III. *Pacif. Coast Avif.* No. 35.
- . 1969b. A study of the Rufous-fronted Thornbird and associated birds (Pts. 1, 2). *Wilson Bull.* 81:5-43, 123-139.
- THOMAS, B. T. 1979. The birds of a ranch in the Venezuelan llanos. Pp. 213-232 *in* *Vertebrate ecology in the northern Neotropics* (J. F. Eisenberg, ed.). Smithsonian Institution Press, Washington, D.C.
- . 1982. Weights of some Venezuelan birds. *Bull. Br. Ornithol. Club* 102:48-52.
- VAURIE, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). *Bull. Am. Mus. Nat. Hist.* Vol. 166:Article 1.

APARTADO 80844, CARACAS 1080-A, VENEZUELA. ACCEPTED 16 JULY 1982.

THE CHIHUAHUAN DESERT RESEARCH INSTITUTE and Sul Ross State University announce the second Chihuahuan Desert Symposium to be held in Alpine, Texas, 20-21 Oct. For information on session topics and submittal of abstracts write DENNIE MILLER, CDRI, Box 1334, Alpine, TX 79830.