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THE BREEDING OF RUFOUS HORNEROS (*FURNARIUS RUFUS*)

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ABSTRACT.—A partially banded population of 12–13 pairs of Rufous Horneros was studied in Buenos Aires Province, Argentina, during 1970–1976. Territories remained relatively stable during the study. Birds lived in pairs and the pair bond usually lasted for more than one breeding season. Territory sizes ranged from 0.25 ha to about 1 ha.

All nesting activities were shared by both sexes. Laying occurred from late August to early December; second broods were attempted in 11 out of 24 nests. Early breeding probably diminished the risks of nest piracy and parasitism by other bird species. Mean clutch size was 3.48 eggs, with individual females showing the whole range of variation (three or four eggs). The incubation period was 16–17 days and the nestling period 24–26 days. Juveniles remained in the parental territories for no less than four months, but they helped occasionally in nest building. Parents opposed this activity.

Asynchronous hatching was observed in all the clutches of four eggs; in 9 out of 13 broods of four the younger nestlings died. Nesting success was high, and an average of 2.52 nestlings were reared per clutch. The annual adult mortality was 28.6%, and thus the population probably produced an excess of juveniles. Territorial behavior apparently played an important role in limiting population density.

In some aspects of its natural history the Rufous Hornero or Red Ovenbird (*Furnarius rufus*) is one of the best known furnariids. However, except for the work of Hermann and Meise (1965), little has been published on other aspects of the biology of the species, such as territoriality, pair bonding and longevity. Certain features, such as the complex nests and asynchronous hatching are of interest beyond the species, itself. The permanent territoriality of horneros may play a role in limiting population numbers, and the existence of prolonged family bonds may have some relevance to current sociobiological ideas.

STUDY AREA

This study was chiefly limited to a small area that was inhabited throughout the study by 12–13 pairs of horneros. The study area is located at the northeastern edge of the main woodland of Estancia La Candelaria, Lobos, Buenos Aires Province, Argentina (35°15′S, 59°13′W) and includes a small adjacent woodland (Fig. 1). The main wood of La Candelaria, which now covers about 60 ha, was planted chiefly between the years 1900–1910, but the first introduced trees were planted more than a century ago. Native trees and shrubs (mostly tala, *Celtis spinosa*, and *Schinus longifolius* and *Sambucus australis*) also grow there.

Area A (2.4 ha) is a lawn with scattered ornamental trees and shrubs. Area B is a tract of untended dense evergreen woodland dominated by *Ligustrum lucidum* and *Acacia melanoxylon*. As both species are naturalized, saplings and young trees are abundant. Except for clearings around recent tree-falls, ground cover is rather sparse and is chiefly composed of the native *Tradescantia fluminensis*. The northern edge of the main wood is planted with large eucalyptus trees (C). Area D is a low, deciduous woodland (about 0.8 ha), originally planted with locust trees (*Robinia pseudoacacia* and *Gleditsia triacanthos*) both of which seed themselves freely. Native talas have invaded this plot. Between area D and the main wood are two old ombú trees (*Phytolacca dioica*) and a group of native shrubs (*Parkinsonia aculeata* and tala). West of area D is a row of old eucalyptus trees.

The study area was surrounded by pasture occupied until 1975 by permanent herds of cattle, sheep and horses that kept the grass short. Later, these plots were plowed. Except for a few scattered trees and shrubs north and east of area D, also inhabited throughout this study by resident horneros, the nearest woodlands are found 1 km north of the study area.

The mean annual rainfall in this part of Buenos Aires Province was 1,072.4 mm (1958–1978); all data on rainfall were obtained at the Instituto Nacional de Tecnología Agropecuaria station at Lobos, 12 km NE of the study area. During 1970–1976 the mean annual rainfall was 986.7 mm. No marked dry season occurs in this part of Argentina. During the study the longest period of dry weather occurred in August–September 1973 (only 13 mm of rain). The drought had adverse effects on the breeding of the horneros, as will be described.

METHODS

Rufous Horneros built 90 nests in the study area between the breeding seasons of 1970 and 1976. All nests built at 5.5 m or less above the ground (N = 24, or 26.7%) were examined. I carved a round hole in the rear wall of the brood chamber, usually before or during the egg-laying period. After each examination, the hole was closed with a short wooden plug and carefully sealed with fresh mud (Fig. 2A). Eggs and younger nestlings were marked with waterproof ink. A sample

of 75 older nestlings was banded with colored celluloid bands and often with additional numbered aluminum bands. Not all the horneros were banded in the same year and of course only a few of those banded in the first year survived throughout this study (see below). In addition, some individuals changed mates and/or left the area. The maximum number of banded individuals present at any one time was 20 (1973). On the average 51.8% of the adult territory owners were banded. I resided in La Candelaria from September to March during the study. In the fall and winter, the longest interval between visits to the study area was 26 days.

In view of the stability of hornero territories during the study, I will often use a territory number to designate a pair or successive pairs of horneros who resided there throughout the years 1970–1975 (e.g., "pair of territory 5").

I distinguished the sexes by their behavior, as follows: Banding showed that in all the nests a single individual of each pair incubated the eggs or brooded the nestlings during the night. For instance, between 1972–1975 the individual gRg of territory 7 was recorded 17 times entering the nest at dusk. I considered these birds female, as did Hermann and Meise (1965). This conclusion is supported by observations of copulation between banded individuals. Female horneros also use a distinctive call to solicit copulation, which is also given in apparently nonsexual contexts.

RESULTS

FORAGING

Rufous Horneros are ground foragers. Seldom have I seen them searching for food on trunks or thick branches. Most of their prey consists of insects and their larvae, but they also eat other invertebrates, particularly earthworms. They usually search for food in places where they can walk, avoiding areas with a uniform, dense ground cover such as tall grasslands and weed-covered fields.

At La Candelaria, Rufous Horneros forage principally in open country, but also in woodland. In the main wood, for instance, several pairs have territories in densely wooded areas where they often search in the leaf litter. Horneros also forage in the woodland of area D, chiefly during the winter when the ground cover is more sparse. In the study area of Hermann and Meise (1965), horneros foraged in wooded areas less frequently.

TERRITORIALITY

Rufous Horneros are strictly territorial. With only minor exceptions (see below), all the activities of the resident pair occur on the territory. Territories are defended throughout the year and both sexes share in defense. Territories and their boundaries were relatively stable during this study (Fig. 1).

Trespassing horneros are expelled by chasing or fighting, with much calling. When chasing an intruder, horneros often

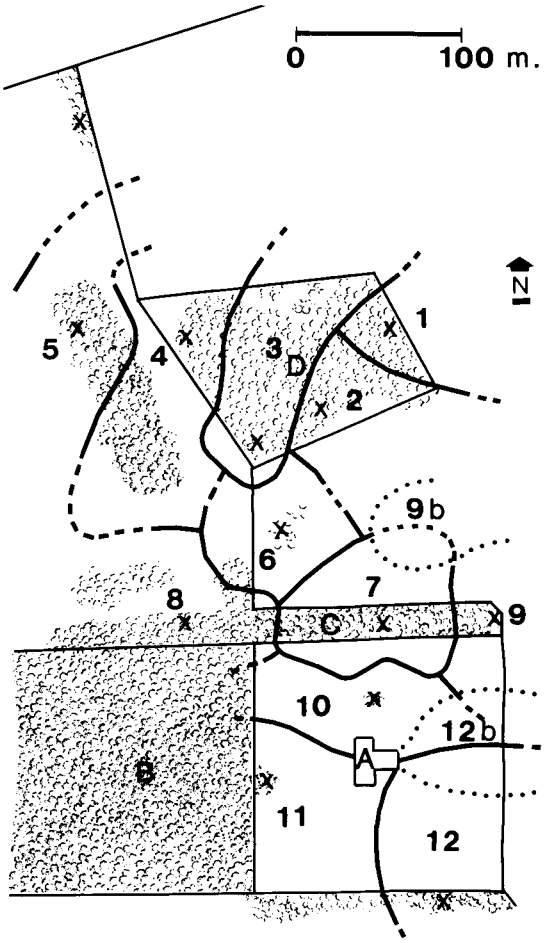

FIGURE 1. The study area and territories (numbered 1–12) of Rufous Horneros in October 1970. The spaces occupied later by territories 9 b and 12 b are also shown (dotted lines). The X's represent the active nests in October 1970. In open areas, territory boundaries are ill defined (dashed lines).

invade other territories, but when the neighboring pair appear, they usually return quickly to their own areas. Territorial conflicts are often followed by outbursts of duetting by each of the pairs involved.

Prolonged territorial conflicts were observed in the study area only when new pairs attempted to establish territories and in a case of extensive boundary shift. In June 1972 four slender wooden poles were placed near the edge of the main wood. Although they were unsuitable as nesting sites, a new pair of horneros (pair 9 b: banded 6 November 1972) built a small, precarious nest on one of the poles in late August. By 8 November they were incubating, but the nest fell to the ground on 22–23 November and the three eggs were destroyed. The male of this pair was seen wandering in the study area until 19 January 1973; the female mated with the male of territory 1.

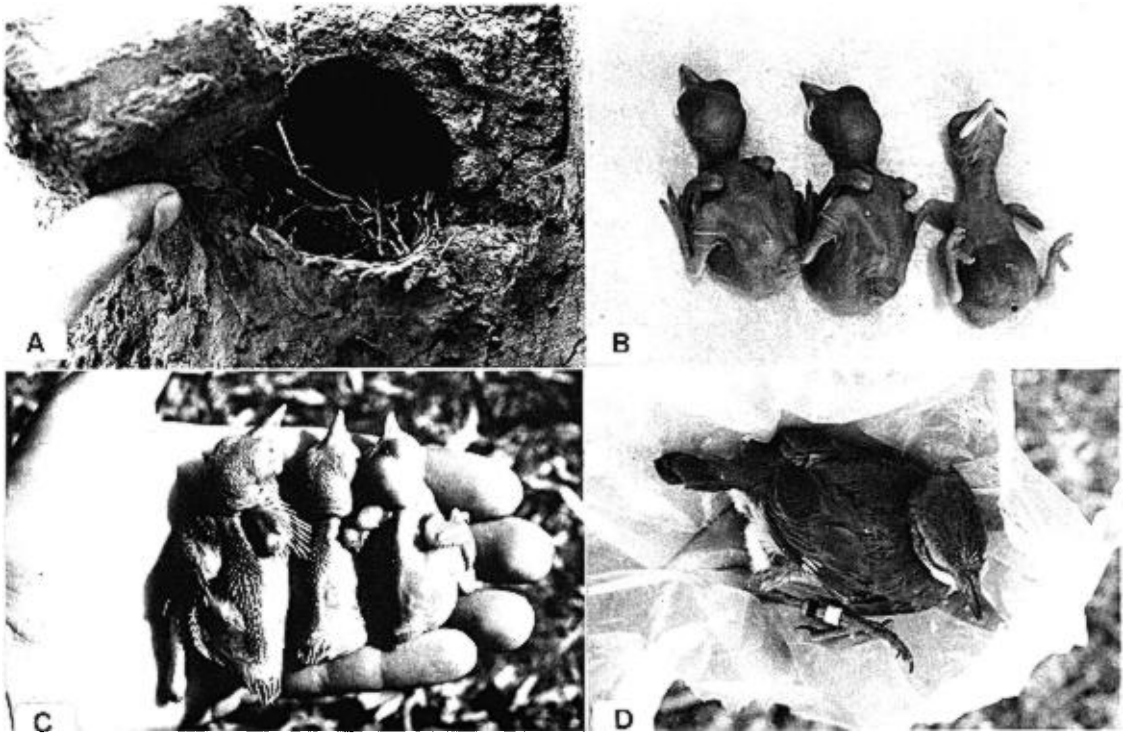

FIGURE 2. A: nest of Rufous Horneros showing observation hole in the rear wall of the brood chamber and the wooden plug. B: two one-day old nestlings and one just-hatched nestling on its back. C: effect of asynchronous hatching in a brood of three nestlings; the nestlings are 7, 6 and 5 days old. D: a 16-day old nestling.

In September 1973 pair 8 attempted to shift its territory well inside territory 6. They eventually started a nest there, when their neighbors were already incubating. Prolonged territorial conflicts were frequent (seen on 19 of 21 days) and the new nest was never finished. In 1975 the pair of territory 6 was nesting in this place.

On 31 July 1973 I observed a new pair of horneros building a nest in a small tala growing at the eastern edge of area A. They raised three fledglings in this new territory (12 b). This female paired with another territorial male in 1974 (outside the study area) but her former mate obtained a new female and remained in territory 12 b.

In June 1976 the pair of territory 7 disappeared and the territory was divided between two neighboring pairs.

Territory sizes in the study area ranged from about 0.25 ha (territory 9 b) to about 1 ha. In the open grasslands around the study area, territorial boundaries were not well defined but the banded horneros were rarely seen fighting more than 150 m away from the woods. Some overlap with neighboring pairs was observed there. In places where the boundaries were better defined, territory sizes ranged from 0.3 to 0.5 ha. Hermann and Meise (1965) reported similar territory sizes.

ROOSTING

The chief exception to strict territoriality is roosting. Rufous Horneros roost in dense foliage. Hence, throughout the winter, they roost only in evergreen trees or shrubs. Some pairs (1, 2, 3) lacked evergreens in their territories; from April to September they roosted outside their territories, chiefly in area B. Pair 9 b had no trees in their small territory and roosted in a palm tree within adjacent territory 9. At dusk these pairs retired later than their neighbors and flew silently in the dim light toward the main woodland.

BREEDING BEHAVIOR

Pair bond. Rufous Horneros pair monogamously and remain paired throughout the year. Banding showed that territorial owners may even pair for life (Fig. 3); two banded pairs (3 and 7) were mated for four consecutive breeding seasons, and another pair (11) for three breeding seasons.

The most striking exception to this monogamy was the male PYRPY of territory 1 (1970–1974), who changed mates shortly af-

ter the end of the breeding season, usually in December or early January. This was not due to an otherwise abnormally high mortality of females in the territory, as two of his former banded mates were seen in the study area soon after these dates. In all these years this male obtained a new mate in less than a month. In 1972 the previous female was noted in the territory on 18 December; the new female, formerly in territory 9 b (see above) was seen on territory 1 on 4 January 1973, duetting with PYRPY. This male showed abnormal nest-building behavior (see later) and never attempted a second brood.

Twice males that lost mates paired with banded females of neighboring territories. In both instances, the females moved to territories where nest sites were more numerous.

Two banded females lost their mates during this study. In 1973 the female of territory 4 also lost her territory, invaded by an unbanded pair (29 June–3 July). In February 1976 the female of territory 3 obtained a new mate and remained in her territory.

Nest. Horneros use mud, mixed with straw, hair, and dung, to build domed nests with a side doorway. A curved entrance tunnel is made by overlapping the outer wall. A lower rim along the floor at the inner end of the tunnel separates it from the more spacious broodchamber. An average-sized nest weighs about 4 kg. Horneros build a new nest each season; I found no exception to this rule during my study.

Nest sites. Horneros prefer relatively thick branches that are close to horizontal, but will also use forks or flat, artificial surfaces. The study area was generally well provided with suitable nesting sites in trees and with a single exception (pair 9 b, 1972) all nests found were built in trees. Suitable nesting sites appeared to be plentiful in territories that included large eucalyptus trees but plot D did not have such a surplus. On the other hand, nests built in eucalyptus and similar trees usually lasted for years (up to eight in some cases) and thus the number of appropriate sites in these territories was somewhat reduced by the presence of old, abandoned nests. In plot D, most nests fell down in less than two years and the old sites were used again in at least five cases. The limiting effect of the old nests was more obvious in a chapel that stood in plot A. Since (at least) 1960 and throughout this study, 15 old hornero nests existed in this building, on the beams under the eaves and/or in the window sills. No further sites were available. In the spring of 1976 the chapel was repaired and most nests were removed. Since then, two pairs of horneros have been nesting in this building (territories 11 and 12 b).

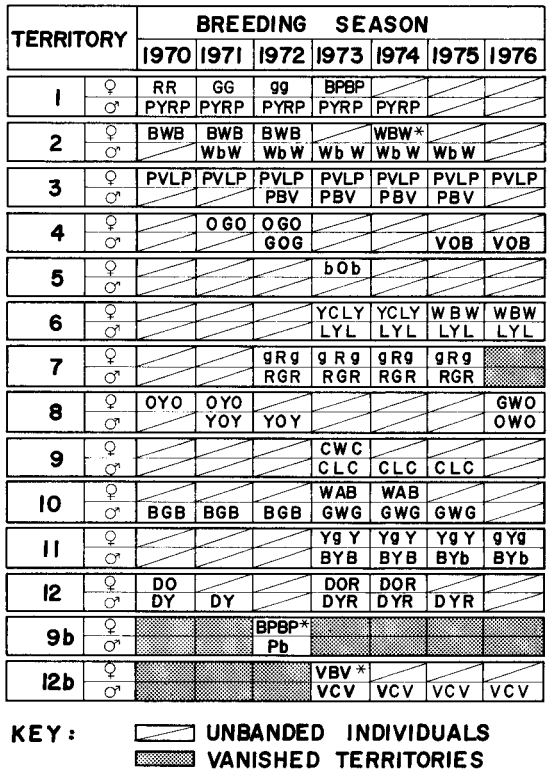

FIGURE 3. Territories and banded horneros in the study area, 1970–1976. The asterisks indicate banded females that deserted mates and changed territories.

In certain situations horneros built new nests on top of old. The birds in the study area were never seen to do this but the pair or pairs that lived in an isolated row of four Lombardy poplars 130 m to the NW usually did so. Nesting sites were probably scarce in these columnar trees.

Nest building. Nest building started at least two or three months before egg-laying. Most pairs began to build their nests between April and June. Nests were finished with the completion of the inner rim, usually a few days before egg-laying. Male PYRPY was also peculiar in that he often began to build his new nests at the end of the previous year. The nest used in 1972 was started on 6–7 December 1971, 18 days after the young left the old nest. The first egg was laid in the new nest on 17 September 1972. He began building the nest for 1973 on 8 November 1972, eight days after the young left the old nest. As he also

TABLE 1. Egg-laying season in Rufous Horneros at La Candelaria.

Period	Number of clutches started		
	First or single	Second broods	Total
16–31 November	1	–	1
1–15 September	9	–	9
16–30 September	5	–	5
1–15 October	8	–	8
16–31 October	1	2	3
1–15 November	–	3	3
16–30 November	–	3	3
1–15 December	–	1	1

changed mates at the end of each year, two females helped in the building of all his nests. In addition, in 1972 he was helped by his young (see below). Such an early start of nest building was sometimes disadvantageous. In the second week of March of 1974 the new nest was so advanced that it attracted nesting Saffron Finches (*Sicalis flaveola*).

Nest building may be delayed in dry weather. This was observed chiefly in the winter of 1973: horneros attempted to collect mud in the territories of other pairs which had access to artificial sources of water. Fresh dung was used more extensively in such dry periods.

Egg laying. The Rufous Hornero is an early breeder among local passerines. In my sample the earliest and latest dates for egg laying were 31 August and 6 December (both in 1975); Table 1 shows the chronology of egg-laying.

In 16 clutches eggs were laid at two-day intervals but once a three-day interval was observed. Laying intervals of two days are probably common among furnariids (Skutch 1969: 296–373).

Clutch size. Rufous Horneros lay either three or four eggs. Most authors have reported clutches of four eggs for the species (e.g., Azara 1802:131; Pereyra 1937:257). Hudson (1920:201) reported a (maximum?) clutch of five eggs from NE Buenos Aires Province, but Gibson (1880, 1918) recorded from this area of Argentina (Estancia Los Ingleses, Cape San Antonio, about 36°25'S) a maximum clutch of four eggs. I found 17 clutches of three and 16 clutches of four giving a mean clutch size of 3.48 eggs. Hermann and Meise reported a mean clutch size of 3.06 eggs (31 clutches).

The observed variation in clutch size was perhaps non-genetic, as four banded females were recorded laying sets of three and four eggs. Mean clutch size was 3.42 eggs in first or single broods (N = 24) and 3.67 eggs in second broods (N = 9), but with this sample size the difference was not significant.

Egg measurements. The average greatest length and greatest width (and standard error) of 23 eggs were 29.23 (0.193) × 21.54 (0.088) mm. The mean weight of 22 eggs was 7.1 g.

According to Schönwetter (1967:10–11), eggs of Rufous Horneros weigh 7 g and their relative weight is 9.3% of the weight of the adult female. However, his figure of 75 g for female horneros does not agree with my data. In my study area the weight of eight unsexed adult horneros was 57.87 (3.30) g (mean and standard deviation). Michael Christie (pers. comm.) found the weight of six unsexed adults from Entre Ríos (Argentina) to be 59.67 (3.23) g. Julio Contreras (pers. comm.) found that 13 females from Mendoza and La Pampa (Argentina) weighed 54.40 (3.10) g. Thus, the relative weight of an egg is close to 12% of the weight of the adult female.

Incubation. Both parents incubate in daytime; only one parent (assumed to be the female) incubates at night. In at least eight cases females slept in their nests during the egg-laying period. In 14 h of observation at five nests, three banded pairs of horneros incubated or remained within the nest 72% of the time. In three hours of observation on 3 November 1971, both members of the pair of territory 5 incubated for almost 100% of the time, but in two hours of observation on the following day, the constancy of incubation dropped to 68%. The longest session I recorded lasted 158 min and the longest period of neglect was 31 min.

The incubation period was 16 days for four clutches (1, c = 3; 3, c = 4) and 17 days for 11 clutches (7, c = 3; 4, c = 4) giving a mean of 16.7 days. The spread of hatching in these 15 sets ranged from six to eight hours to no less than 48 h. Hermann and Meise reported incubation periods of 14–18 days. The eggshells were promptly removed.

Nestling period. Both sexes feed the nestlings at roughly equal rates. The parents bring food in the tips of their bills. Some identified items were crickets, mole crickets (*Scapteriscus*), larvae of soil beetles, caterpillars, spiders and earthworms. Observed feeding rates ranged from 2.3 items per nestling per hour (one-day old nestlings) to 8.8 items per nestling per hour (16-day old nestlings). Both parents brood the nestlings in daytime. The time spent in brooding gradually decreases during the nestling pe-

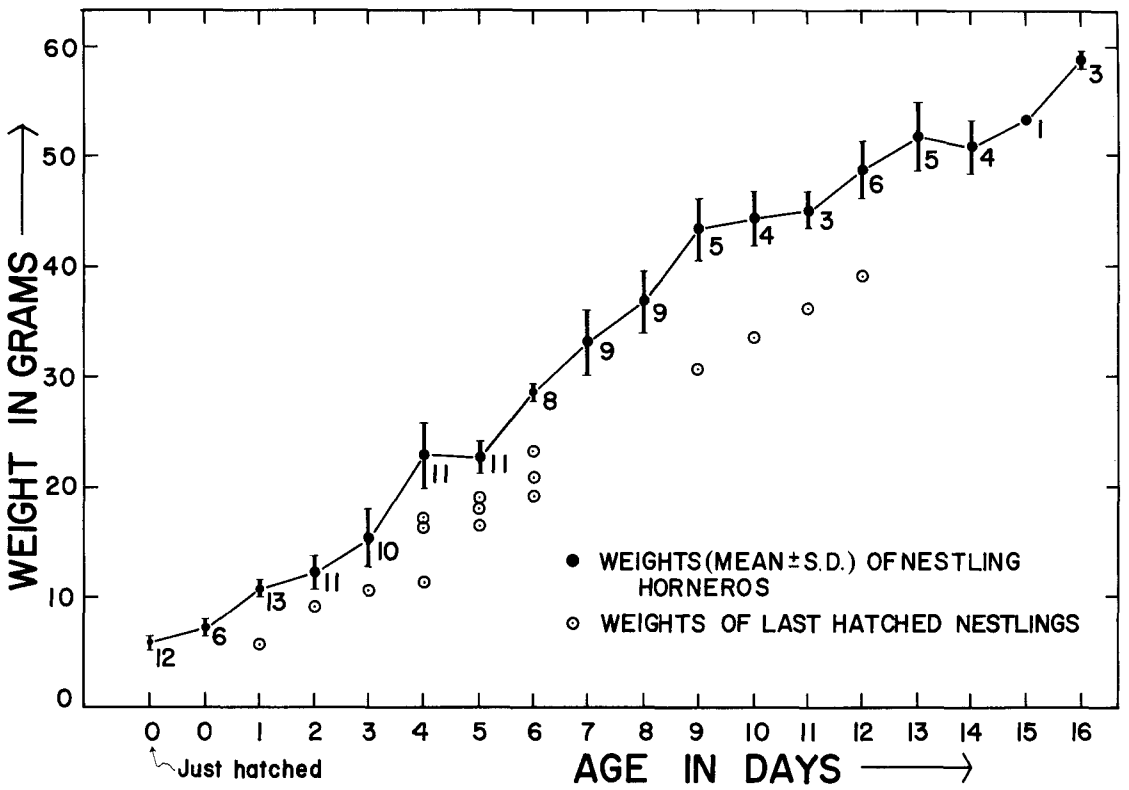

FIGURE 4. Weights of nestling Rufous Horneros. The numbers below the black dots indicate sample size. The weights of some last-hatched nestlings in broods of four nestlings are also shown.

riod but some diurnal brooding was observed until day 12. Females were recorded sleeping in the nest until day 15–17 of the nestling period. After day 9, the parents frequently do not enter the nest when feeding the nestlings, but remain clinging to the doorway like woodpeckers. From day 5, fecal sacs were carried away by both sexes.

The recorded nestling period was 24–26 days; 10 nestlings departed at day 24, nine nestlings at day 25 and 16 nestlings at day 26 ($\bar{x}$ = 25.2 days). According to Hermann and Meise the nestling period was 21–26 days, but their method of examining nests may have caused premature departures.

Development of nestlings. Newly-hatched horneros are naked (Fig. 2B). The mouth lining is yellow and the flanges are pale yellow. Their mean weight at hatching (Fig. 4) is 83.9% of the mean egg weight.

The nestlings begin to open their eyes at days 4–5, but until day 9 the eyes are closed most of the time. Feather tracts become visible as darker lines in the skin at day 3. Pinfeathers visibly project from the skin at day 5. The first feather tips are seen on day 7 in the pinfeathers of the dorsal tracts. At day 9–10 almost all the pinfeathers are sprouting except those of the capital tract. At this time nestlings have conspicuous pale yellow oral flanges, pale gray feet and grayish bills. The eyes are brownish (not reddish brown as in the adults), with bluish-gray reflections in some lights. Nestlings are almost wholly feathered at day 16–17 (Fig. 2D). Older nestlings have smaller flanges and their most conspicuous feature in the dark interior of the nest is their white throats.

At day 3–4 nestlings may crawl when placed on the ground. From day 4 onwards they squat with raised heads; inside the nest they assume the same posture with the head resting on the wall or the inner rim of the nest. Wing-flapping was observed at day 9. If placed in a sunny spot on the ground, 16-day old nestlings crawl restlessly, but remain quiet in the shade.

During the last week of the nestling period the vocalizations of the young horneros can be heard at considerable distance from the nest. Nestlings about to leave the nest frequently answer parental calls and may even attempt to duet with a parent.

Weights of nestling horneros are given in Figure 4. The intrinsic rate of growth calculated from data in the table by the method of Crossner (1977) was 0.3146 g/day per g; last-hatched nestlings were excluded, as

was the category "just hatched." Young horneros weigh about as much as adults when they leave the nest.

Replacement nests. If a nest is damaged or pillaged a replacement nest is built rather quickly in another site. In this study only two pairs of horneros built replacement nests. On the night of 6–7 September the nest of one pair fell to the ground. The horneros built a new nest in about 12 days, and laid four eggs between 20–26 September. Only the first two eggs hatched after an abnormally short incubation period of 14 days.

Second broods. Second broods appear to be common in this species, although Hermann and Meise (1965) did not record any in Santa Fé. Second broods occurred in 11 of 24 nests examined in my study, although only nine were followed in detail. The second clutch was always laid in the same nest. In five cases the intervals between the departure of the young of the first brood and the laying of the first egg of the second set ranged from 6 to 19 days (mean: 10.5 days). Some pairs always attempted second broods (e.g., pair of territory 3) and others never did (male PYRPY and his mates).

Nesting success. Of the 115 eggs laid in 33 clutches seven eggs did not hatch. Two of these were laid in a replacement clutch and dead embryos were found in at least three eggs. A whole set of four eggs was lost in a nest that fell to the ground. Predation on eggs was not observed.

Starvation seemed to be the major cause of nestling mortality, as 14 nestlings that disappeared during the first 10 days of the nestling period probably starved. Starvation was particularly common among the last-hatched nestlings in broods of four; 9 out of 13 such nestlings starved. Even when they survived, these nestlings weighed less than the mean weight (Fig. 4). Rufous Horneros in the study area often were unable to rear more than three nestlings. The spread of hatching in clutches of four was never less than 24 h. Asynchronous hatching has usually been regarded as an adaptation for reducing brood size during fluctuations of the food supply (Lack 1954:40–41). Only 2 of 14 last-hatched nestlings in broods of three died of starvation; the difference from broods of four is significant ($P < 0.01$). This pattern of mortality strongly suggests starvation. In September–October 1973 after or during a dry period (see above) a brood of three nestlings starved and disappeared in four days; this brood is excluded from the previous calculations. The maximum weight attained by the nestlings was 8 g. The pair successfully reared four fledglings in the same nest in November.

Nestlings of two pairs were preyed upon on 9 and 10 December 1972 by a young white-eared oppossum (*Didelphis albiventris*). I found the predator inside the nest on territory 2 with the partially eaten corpses of the female and the nestlings.

Estimates of nesting success were as follows: nestlings/eggs, 104/115 or 90.4%; fledglings/nestlings, 83/104 or 79.8%; fledglings/eggs, 83/115 or 72.2%. An average of 2.52 fledglings was reared per clutch. The ratio fledglings/eggs did not differ significantly between clutches of three and four eggs. Hence, clutches of four are only slightly more productive than clutches of three.

These figures for nesting success are the highest I have found among local passerines. Assuming that one-third of the breeding pairs attempted second broods, an average of 3.35 fledglings were reared per pair per season.

THE POST-FLEDGING PERIOD

Fledgling stage. Fledgling Rufous Horneros have shorter bills and more slender bodies than their parents. After the prolonged nestling period, the post-fledging period of dependence is comparatively short (about three weeks). In the first three to four days after leaving the nest, fledglings remain perched somewhere in the parental territories, begging food from both parents. At day 5–6 the fledglings begin to follow their parents to open country and probably find some food by themselves. In the following two weeks the young slowly become independent. I have seen young horneros begging food from their parents 20–21 days after leaving the nest, but they usually were ignored.

Young horneros begin to utter alarm calls three to five days after leaving the nest. Soon they call in alarm at the slightest disturbance. Young horneros duet frequently with their parents and siblings.

Independent young horneros often wander briefly in neighboring territories and frequently join other juveniles. As long as they remain silent, they are likely to be ignored by the resident horneros.

The young as helpers in nest building. On 7 December 1971, while I was watching the nest-building activities of male PYRPY, I saw one of his young (fledged on 18 November 1971) carry fresh cow dung to the foun-

dations of the new nest. On the following days I observed two young helping in nest building. Between 9 December 1971 and 19 January 1972 in six discontinuous hours of observation, the male parent made 11 trips to the nest, one young 6 trips, the other young 4 trips, and the female 5 trips (she soon disappeared). The young horneros not only carried mud or cow dung to the nest, but also pecked at some disturbing leaves that were growing near the foundations. The male parent supplanted one young who was building on one occasion and this young supplanted its sibling who was building on 5 occasions. The young were never chased away from the nest site and remained perched in nearby branches. In the following years this male was intolerant of the young and often chased them from the new nest site. This behavior is probably more typical of parent horneros.

I saw only one other instance of cooperative nest building by young horneros. On 4 August 1974 one banded young flew to its parents' new nest with mud, but on the following day only the parents were building.

Pairing and nest building in young horneros. On 17 August 1974 I observed one banded young of territory 6 (hatched 29 September 1973) carrying mud to the top of a slender wooden pole placed between territories 6 and 7 (in the same area of the territory 9 b of 1972). Here it was joined by a young of territory 7 (hatched 30 November 1973). The juveniles behaved as a mated pair. They brought mud to the foundations and duetted frequently there. Once they chased away another young bird of territory 7. At this time of the year the pairs of territories 6 and 7 were already antagonistic to their young and in the following days building activity on the pole was not as frequent. Both juveniles vanished from the study area between 14–16 September 1974. They could have bred in that season.

Departure of the young. Parents attempting second broods became increasingly intolerant of the young of their first brood. In most cases the latter were eventually expelled from the territory one or two weeks before the departure of the new nestlings. With a few exceptions, I never saw them again in the study area. An interesting exception to this occurred in 1975 when the pair of territory 10 attempted its second brood after having reared three fledglings from the first. Only a single egg hatched in the second set and, although the older young were chased away or supplanted from the area of the nest tree, they were allowed to remain elsewhere in the territory. In June 1976 the four young of the two broods were still with their parents.

Young horneros, either from single or second broods, remained with their parents four to nine months. The most intolerant pairs expelled their young in late April or early May. Other pairs became aggressive to their young only at the start of the next breeding season, in late August or September. Until they left the parental territories, young horneros had a low mortality rate. Of 41 banded juveniles (1970–1974), at least 32 (78%) were alive four months after leaving the nest.

Only two horneros banded as nestlings were later recorded as established in the study area or elsewhere in the main woodland of La Candelaria. The female WAB (hatched 24 October 1970, pair of territory 1) was mated to the male of territory 10 on 14 February 1972. She reared one brood in 1973, and two broods in 1974 but disappeared in June–July 1974. The male CLAVB (hatched 10 October 1973, pair of territory 12 b) obtained a territory in the main woodland south of the study area during June 1975. Another banded juvenile of unknown sex (hatched on 18–19 November 1972 in territory 3) was found on 15 February 1973 in a seasonal marsh 600 m west of the study area; it was apparently paired and defended a possible nesting area in a row of half-submerged fenceposts. It disappeared in April 1973.

Adult survival. The minimum average annual survival rate of territory owners was 71.4%; banded individuals with precarious territories (e.g., pair of territory 9 b) and the successive mates of male PYRPY were excluded from the computations. The average life expectancy (Lack 1954:93) was three years for territory owners. As of 1978, five horneros in the study area have survived more than four breeding seasons since banding.

Due to their low mortality rate, Rufous Horneros in my study area produced an excess of juveniles. The mortality of the juveniles after leaving the parental territory was possibly higher than the mortality of territorial adults, but even so the existence of a "floating" population is suggested by the data on the replacement of territory owners.

OTHER BIRD SPECIES USING HORNERO NESTS

On the whole, Rufous Horneros are early

breeders and only the pairs which breed during October or later may have to interact with birds of other species, including brood parasites. This is one of the possible advantages of early breeding.

Nest piracy. In La Candelaria at least five species of passerines may use nests of horneros for breeding or roosting. Only one case of nest piracy was noted. In November 1977 a pair of House Sparrows (*Passer domesticus*) usurped a nest (in a building) in which a pair of horneros was about to attempt a second brood. Burger (1976) recorded other cases of nest piracy involving House Sparrows.

Brood parasitism. Screaming Cowbirds (*Molothrus rufoaxillaris*) visited active nests of horneros in La Candelaria. In August 1975 in less than six hours of observation an unfinished nest was visited twice by up to three pairs of Screaming Cowbirds. I found no eggs of this cowbird in the hornero nests.

The Rufous Hornero has been recorded as a host of the Shiny Cowbird (*Molothrus bonariensis*; Friedmann 1929:94–97). In Friedmann's sample, 18 of 61 active nests were parasitized. Most records of parasitism were from the northern provinces of Argentina (see also Wilson 1979). Hermann and Meise (1965) recorded two cases of parasitism, one of which was successful, in their study area in Santa Fé. Records of parasitism from Buenos Aires Province are from the NE coast (Gibson 1880, Paul Mason, pers. comm.). I have no records of Shiny Cowbird eggs in active nests of horneros, and I have not seen horneros rearing or even casually feeding young cowbirds in La Candelaria.

According to Hoy and Ottow (1964), Rufous Horneros are possible ejectors of cowbird eggs in Salta, Argentina, and one case reported by Hermann and Meise is also suggestive. I performed experiments to test the point; all the spotted Shiny Cowbird eggs (N = 7) were ejected, as well as three out of four unmarked Shiny Cowbird eggs. Eggs of Rufous Horneros are white and unmarked. Horneros also ejected two eggs of Screaming Cowbirds and three eggs of House Sparrows. The ejected eggs were found in the entrance tunnels or on the ground under the nests.

Shiny Cowbirds at La Candelaria start visiting host nests and laying eggs in the last week of September. If cowbirds were removing hornero eggs I should have found a decrease in clutch size in the later sets, particularly in second broods. Actually I observed the reverse.

DISCUSSION

COMPARISONS WITH OTHER STUDIES

In this section I compare my findings with those of Hermann and Meise (1965). Unfortunately, our studies are not always strictly comparable, as Hermann and Meise gathered data during a single breeding season. Their study area was located in Estancia Las Chilquitas, Las Rosas, Depto. Belgrano, Provincia de Santa Fé, Argentina (32°23′S, 61°42″W). Both study areas are in the rather uniform Pampean region of Argentina. Mean winter temperatures are similar at both sites; although La Candelaria is farther south, it is closer to the Atlantic Ocean. Summers are warmer in Las Chilquitas and mean January temperatures are almost 2°C higher. The mean annual rainfall is less at Las Chilquitas (875 mm).

Nest sites. In a sample of 536 nests (old and new) from Las Chilquitas, 330 nests (61.6%) were built in trees, 174 nests (32.5%) were built on poles and fenceposts, and 32 nests (5.9%) were built in buildings and other sites. Two nests (0.4%) were built on the ground. In my study area 89 out of 90 nests were built in trees, and only one nest was built on a pole; fenceposts were not used as nest sites. In La Candelaria these nest sites were apparently suboptimal and were used chiefly by pairs that lacked appropriate nest trees within their territories. Most nests studied by Hermann and Meise were built on fenceposts.

Nests built on the ground have also been reported from other places (e.g., Gibson 1880, 1918: three cases in 39 years). With the usual abundance of terrestrial predators, these nests are likely to be deadly for nestlings and adults.

Breeding season. Gibson (1880) found hornero eggs in Cape San Antonio, Buenos Aires Province, from mid-September to the end of December. The breeding season at La Candelaria was similar. In Las Chilquitas, hornero eggs were recorded from 10 September to 29 November, the last nestlings were fledged by mid-December, and no second broods were detected. Dieselhorst and Hermann (1958) claimed that the high temperatures of December–January limited the duration of the breeding season at Las Chilquitas. The higher temperatures recorded within the nests were regarded as a cause of mortality for eggs and nestlings.

Clutch size and brood size. As with most passerines in La Candelaria, Rufous Horneros lay three or four eggs. Avian clutches are smaller in southern South America than in the northern temperate regions (Cody

1966). Two important factors that may explain the difference are reduced food supply (Lack 1954, 1968) and increased nest predation (Skutch 1949, Foster 1974). The first factor seems more important for Rufous Horneros, at least in my study area.

Hermann and Meise sampled the arthropod fauna of 1 m^2 of grassland and concluded that food was not a limiting factor for breeding horneros. Objections could be raised against their method and conclusions. The sampling was done in October 1956, with a rainfall of 201 mm; the average rainfall for that month was 88 mm in Las Chilquitas (data in Diesselhorst and Hermann 1958). Probably not all the sampled arthropods were appropriate food for nestlings and it is not known what proportion of these arthropods could have been harvested by the horneros in a given period of time.

Mean clutch size was smaller in Las Chilquitas than in La Candelaria (3.06 vs. 3.42 eggs); clutches of four eggs were significantly less common in Las Chilquitas (2 out of 31 vs. 16 out of 33 sets, $P < 0.005$). The small difference in latitude probably cannot account for such a large difference in clutch size. In La Candelaria 11 sets of three eggs were laid by females who were perhaps breeding for the first time but this is a tentative hypothesis.

Brood reduction was not observed at Las Chilquitas.

Nesting success. Nesting success was significantly lower at Las Chilquitas (ratios fledglings/eggs: 35/95 vs. 83/115, $P < 0.005$). Further comparison reveals a highly significant difference in egg mortality (ratios nestlings/eggs: 54/95 at Las Chilquitas vs. 104/115 at La Candelaria, $P < 0.005$), and a smaller, non-significant difference in nestling mortality. The productivity per pair was 1.3 fledglings at Las Chilquitas.

Hermann and Meise recognized that their figures for nesting success were applicable only to nests built at lower heights, particularly on fenceposts. These nests were frequently destroyed by humans, cattle and horses at Las Chilquitas. Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*) destroyed one nest and removed the nestlings. Otherwise most nest predators recorded at Las Chilquitas also occurred at La Candelaria.

Hermann and Meise estimated that only one out of 30 pairs of horneros nesting in trees in their study area failed to produce fledglings. My findings agree closely with their estimate. The comparison of both studies shows the consequences of using optimal and suboptimal nesting sites. This point is relevant to any discussion on the adaptive value of the complex nest of the species.

FAMILY BOND AND HELPING

The occasional cases of helping among horneros do not fit easily into the recent classification of avian communal breeding systems proposed by Brown (1978). Rufous Horneros may approach a TS (territorial, single breeding) type of communal breeding, but the juveniles helped their parents (and eventually their future siblings) only in nest building. Kinship may be important in the evolution of communal breeding, but other factors may be equally relevant. It is obvious that in my study area adult horneros were able to build nests without the assistance of their offspring. Perhaps in areas with a low and unpredictable winter rainfall (e.g., the Chaco), adults may benefit from this help, and encourage this behavior. However, the rather precocial pairing behavior exhibited by some young horneros may well prevent further evolution of a communal breeding system.

RUFOUS HORNEROS AS NEOTROPICAL BIRDS

Rufous Horneros share several features of their breeding biology and ecology with most neotropical passerines and land birds. Their low adult mortality rate is well within the range recorded for several species of neotropical passerines at lower latitudes (Snow and Lill 1974), showing that this trend may also occur at higher latitudes in South America. Rufous Horneros may have, however, a higher nesting success than most tropical forest birds (but see Oniki 1978). The figures for my study area are similar to estimates of nesting success of hole-nesting passerines breeding in the northern temperate regions (Lack 1954:74–87, Cody 1971). The Argentine Pampa lacks some types of arboreal nest predators (particularly arboreal snakes) that are common at lower latitudes, but even so, this combination of low mortality and high productivity is unusual among local birds.

TERRITORIAL BEHAVIOR AND SURPLUS BIRDS

Rufous Horneros in La Candelaria were probably living at levels 2 and 3 of population density (Brown 1969). At level 2, territorial behavior forces some individuals to settle and nest in suboptimal habitat; at level 3 the optimal and suboptimal habitats are occupied by territorial owners, and the remaining individuals exist as non-breeding floaters. In my study area the suboptimal

and unfavorable habitats offered, respectively, few or no suitable nest sites, similar, perhaps, to Las Chilquitas. The occasional cases of ground nesting among horneros do not contradict this view; probably this activity is too risky for the breeding adults.

Smith (1978) has discussed the possible habits and organization of floaters. Flocks of surplus horneros ("strategy 1") have not been reported in any study of the species. My limited data suggest that surplus horneros live singly ("strategy 2"), and perhaps as loose pairs. Surplus horneros may have restricted home ranges. The female in territory 10 in 1973–1974 was seen three times in the study area during 1972.

SUMARIO

Se estudió una población parcialmente anillada del Hornero (*Furnarius rufus*) en una zona de la Provincia de Buenos Aires, Argentina, entre los años 1970–1976. Los territorios permanecieron relativamente estables durante el estudio. Los horneros con territorios vivieron en parejas en las que el vínculo persistió usualmente por más de una temporada de cría. El tamaño de los territorios osciló entre 0.25 y aproximadamente 1 ha.

Las actividades de nidificación fueron compartidas por ambos sexos. La postura de huevos tuvo lugar entre el fin de agosto y el comienzo de diciembre; en 11 de 24 nidos se intentaron segundas posturas. La postura promedio fue 3.48 huevos con variaciones individuales que cubrieron todo el rango de 3 a 4 huevos. El período de incubación fue 16–17 días y el de permanencia en el nido 24–26 días. Los jóvenes permanecieron en sus territorios natales durante al menos 4 meses, ayudando ocasionalmente a sus padres a construir nidos.

El éxito de cría fue alto, produciendo cada pareja 3.35 jóvenes por temporada de cría en promedio. La causa principal de mortandad de pichones fue el hambre; los pichones más jóvenes perecieron en 9 de 13 polladas de 4. La mortandad anual de adultos fue 28.6%. La población produjo probablemente un exceso de jóvenes. La conducta territorial parece tener un rol importante en la limitación de la densidad de población.

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