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REPRODUCTIVE ECOLOGY OF THE RUDDY GROUND-DOVE ON THE CENTRAL PLATEAU OF BRAZIL

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ABSTRACT.—The reproductive ecology of the Ruddy Ground-Dove (*Columbina talpacoti*) was studied between January 1982 and February 1983 in the Cerrado of the Central Plateau of Brazil. A total of 218 nests were found in 19 plant species, at heights ranging from ground level to 7.5 m. Nest construction was observed in all months except October. Some pairs reared a second clutch in the same nest in the same year. There was no significant difference between the sexes in nest defense behavior. The median clutch size of 200 nests was two. Fledglings remained with their parents for 25 days. One reached sexual maturity three months after hatching. The average daily mortality rate of eggs based on the Mayfield (1961, 1975) method was lowest (2.8%) in April–May and highest (8%) in November–December. The mean rate of daily egg mortality rate in all nests over the year was 4.4%. The total daily mortality rate of nestlings was (3.8%), ranging from (1.0%) in August–September to (5%) in February–March. There was a significant difference in the rate of predation on eggs and on nestlings. The highest rate of predation occurred during the peak of fledgling production. The probability of a nestling remaining in the nest until fledging was 63.3% and the probability of the nestling surviving from laying to fledging was 36.7%. At the end of incubation, there was an average of 1.2 eggs per nest and a mean of 0.7 nestlings per nest fledged. *Received 24 Aug. 1987, accepted 5 Jan. 1988.*

The Ruddy Ground-Dove (*Columbina talpacoti*) ranges from southern Texas (Shifflet 1975) to northern Argentina (Meyer de Schauensee 1966.) It can be found in natural habitats, such as forest, cerrado, and marshes, as well as on ranches and farms. Although the biology of the Ruddy Ground-Dove has been studied (Haverschmidt 1953, Skutch 1956, Carvalho 1957, Trollope 1974, Oniki and Willis 1983), little is known of the nesting ecology and reproductive success of the species. Much of the available literature is qualitative, and none involves studies over the entire breeding season. In the present paper I present quantitative data on nests, eggs, clutch size, nest defense, nestlings, fledglings, and breeding success of a population of Ruddy Ground-Doves in Brazilian cerrado.

STUDY AREA AND METHODS

The study was conducted between January 1982 and February 1983 on Fazenda Agua limpa, 30 km south of Brasilia, Brazil (15°55'S, 48°00'W). In Brasilia there are two climatic seasons: the dry season between June and September, and the wet season from October to May. The study area comprised 6.5 ha, of which 2 ha was coffee plantation (*Cupressus* sp.), and 2.5 ha cerrado (savanna woodland).

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Nests found before or shortly after egg laying were visited daily. The entire area was searched for nests every two days. Eggs, nestlings, and adults were measured using vernier calipers (0.1 mm) and pesola spring balances (0.2 g precision). The daily mortality rates and success probabilities of nests were calculated following Mayfield (1961, 1975), and I used only those nests with two eggs or nestlings. Food habits of nestlings were determined through direct observation of crop contents. To evaluate nest defense, dead frozen males and females in standing posture were put at varying distances from nests. The reactions of nest owners were observed through binoculars at distances of 20–50 m. Nestlings were banded with numbered metallic bands (IBDF-Cemave Brazil). Doves were captured in mist nets erected in places that flocks frequented. Statistical methods follow Snedecor and Cochran (1967) and Sokal and Rohlf (1981).

RESULTS

Nest characteristics.—I observed nest construction in all months except October. Nests constructed in September remained active until mid-October. Courtship was also observed in October. There was less nest activity during the final months of 1982, and in January 1983 the number of active nests increased again. The breeding season started in January and finished in September with few pairs nesting in November and December. Two hundred and eighteen nests were found from ground level (in cerrado) to a height of 7.5 m (in cypress), and from between zero to 4.5 m away from the center of the tree. Most nests (90%) were constructed in forks of horizontal limbs, which are quite common in cypress trees. Nests were constructed in 19 different plant species, and the distribution of nests among plant types differed significantly ($\chi^2 = 24.07$; $P < 0.0001$; df = 17) from that expected on the basis of the numbers of each plant species present (Table 1). The greatest number of nests occurred in cypress trees despite the fact that only 31.7% of the trees in the area were of this species. Of the other nests, 25.5% were built in coffee trees and the remaining were built in 17 different plant species. Four nests were built on the ground (Table 1). The principal material used in the construction of nests was the grass *Brachiaria plantaginea.* Three nests were constructed with roots and the others (N = 215) with stems and leaves of the grass *Brachiaria.* Only males were observed carrying material to nests. They made as many as 13 trips per min for up to 2 h at a time. Females arranged the material in the nest. Nest construction required an average of 4 days. The females roosted overnight in the empty nests prior to egg laying, and generally laid their first egg on the day after the nest was completed. They began incubation the following morning. Nests resembled small flat, elliptical shells. The mean external length of 27 nests was 109.8 mm ± 11.6 (range 91–135); the mean external width was 93.1 mm ± 13.1 (70–117); and the mean external height was 35.6 mm ± 8 (26–60). In nests the mean internal length was 68.5 mm ± 8.7 (55–80), the mean internal width was

TABLE 1
LOCATION OF *COLUMBINA TALPACOTI* NESTS RELATIVE TO THE NUMBERS OF VARIOUS PLANTS IN THE STUDY AREA

Plant species	Number of plants	Percent	Number of nests	Percent
Ciprest (*Cupressus* sp.)	864	31.7	145	53.5
Café (*Coffea arabica*)	1600	58.6	69	25.5
Feijao espada (*Canavalia gladiata*)	140	5.1	9	3.3
Maracujá (*Passiflora* sp.)	30	1.1	8	2.9
Mangueira (*Mangifera indica*)	1	0.03	7	2.6
Palmeira (*Syagrus* sp.)	1	0.03	7	2.6
Laranjeira (*Citrus* sp.)	1	0.03	4	1.4
Chuchú (*Sechium edule*)	1	0.03	4	1.4
Ground of cerrado	4	0.15	4	1.4
Limoeiro (*Citrus* sp.)	3	0.1	3	1.1
Laranjinha do cerrado (*Styrax ferruginea*)	19	0.7	2	0.7
Milho (*Zea mays*)	50	1.8	1	0.4
Jaqueira (*Artocarpus integrifolia*)	1	0.03	1	0.4
Coragão de negro (*Connarus fulvus*)	1	0.03	1	0.4
Palmeira (*Syagrus flexuosa*)	1	0.03	1	0.4
Bananeira (*Musa* sp.)	4	0.15	1	0.4
Urucum (*Bixa orellana*)	2	0.07	1	0.4
Ficus (*Ficus elastica*)	1	0.03	1	0.4
Mexicrica (*Citrus* sp.)	1	0.03	1	0.4
Jamelao (*Eugenia cumini*)	7	0.2	1	0.4
Total	2728	100	271[a]	100

[a] Only 218 nests were used to calculate reproductive success.

5.93 mm ± 1.7 (55–60), and the internal height averaged 27.1 mm ± 3.6 (26–30).

I observed three pairs reusing nests. Successive clutches were produced up to three times in the same nest. The pairs only added a little more material on the upper part. Only successful nests were reused. If predation occurred, the nest was abandoned. Nearby new sites (<5 m away) were chosen in five cases.

Eggs and incubation.—Egg white differed significantly among eggs during the breeding season ($F_{6 \pm 140} = 188$; $P < 0.0005$; df = 146). The mean length of 85 eggs was 22.4 mm ± 0.10 (20–24.5 mm), mean width 16.8 mm ± 0.06 (15.2–18.5), and mean weight 3.41 g ± 0.05 (2–4.2 g). Of 218 nests, 91.7% contained two eggs (or nestlings), 7.8% contained one egg (or nestling), and 0.5% had three nestlings. The maximum number of clutches (each with two offspring) reared by one pair in the same year was four (N = 3).

Females began incubating after laying the first egg. The average period from the laying of the first egg to the hatching of the last egg in the nest was 12 days. Observations of two pairs indicate that the female incubates for approximately 18 h daily and the male for 6 h. The daily pattern of incubation at two nests was: at 07:00 h the female leaves and the male commences, at 11:00 h and 13:00 h the sexes switch, and at 15:00 h the female returns and remains until the following morning. Both the male and female displayed the same behavior before replacing the mate at the nest. After perching near the nest but on another limb, the incoming bird flew to the limb supporting the nest, walked to the nest where it remained still for a few seconds beside its mate. The sitting bird stood and walked to the limb's tip and flew away while the other immediately sat upon the nest. Neither during the period of incubation, nor during the growth period of the nestlings, was the nest left unattended.

Nest defense.—In 6 of 21 tests of response to artificial birds the nesting bird attacked the model, jumping on its back and pecking its head. In 10 tests there was no reaction from the sitting bird. The nesting bird remained near the nest (1–2 m) on the ground while the model was present in 5 tests. Both reactions occurred in nests from the time of construction to when they had 5-day-old nestlings. The reactions of males to male models were not significantly different from the females' reactions to female models ($\chi^2 = 0.24$; $P > 0.50$; df = 1; N = 10). Indifferent reactions to the model were more frequent between midincubation and the nestling growth stage (when the nest was guarded by the adults) than during the initial incubation period; however, the difference was not significant ($\chi^2 = 0.28$; $P > 0.50$ df = 1; N = 10). Intraspecific aggression was also observed in the field when neighboring males were seen batting their wings against one another while chasing each other in flights near nests under construction.

Hatching, nestling, and fledgling.—Hatching generally seems to be synchronized. After the eggs hatch, the parents carry the shells in their bills approximately 6 m (N = 2) from the nest. Hatchlings are altricial, their eyes closed at birth. Their naked bodies have a single narrow dorsal strip of buff colored feathers. The beaks are grey with a black narrow band separating the completely white tip. The white tip and the black band completely disappear when the young are ready to fledge. At 3 days after hatching, the nestling's eyes open and the birds begin to chip softly ("peebe") (N = 10). Food is regurgitated by the parents on the first day when the nestlings receive only "crop milk." On the following day they are fed small seed fragments (*Paspalum* sp., *Brachiaria plantaginea,* etc). The larger seeds (e.g., *Sorghum* sp., wheat, and rice), were observed in nestling crops after 4 days (N = 4). Analysis of variance showed no significant differences in the weight at hatching among the nestlings that: (1) hatched

in different periods of the year ($F_{3,45} = 1.46$; $P > 0.10$; df = 52); (2) hatched in a nest alone or with one other nestling ($F_{2,49} = 0.16$; $P > 0.10$; df = 52); (3) hatched in nests localized in a coffee plantation or in a cypress grove ($F_{1,45} = 0.63$; $P > 0.10$; df = 52); (4) hatched in the dry or rainy season ($F_{1,38} = 0.48$; $P > 0.10$; df = 90). Measurements of one-day-old nestlings were: bill length 6.1 mm ± 0.03, N = 126; tarsus length 5.5 mm ± 0.1, N = 51; wing length 8.5 mm ± 0.1, N = 126 and body weight 3.2 g ± 0.1, N = 126. Nestlings remained in the nest from 9 to 15 days; $\bar{x}$ ± SD = 11.8 days ± 1.3 (N = 99). Fledglings had a bill length of 11.7 mm ± 0.07, N = 83; a tarsus length of 13.8 mm ± 0.26, N = 23; a wing length of 58.0 mm ± 0.74, N = 83; and a body weight of 24.8 g ± 6.0, N = 83. Up to the fifth day after leaving the nest, the fledglings still received regurgitated food from their parents (N = 3). After this, the fledglings began to peck the ground to pick up seeds. Fledglings left the nest with a weight that averaged 47% of their paternal parent's and 50% of their maternal parent's. Two young remained with their parents (who fed them frequently) for 25 days after leaving the nest (observations were made for one pair). Following this period, the young formed flocks and became independent.

Age at first reproductions.—One three-month-old male banded as a nestling was found incubating eggs in a nest, suggesting that sexual maturity can be reached within 3 months after hatching. Consecutive captures of one male (in the third, fifth, sixth, and eleventh month after having left the nest as a fledgling) showed that after only 3 months of age, it reached 97.7% of the average weight of an adult.

Adult weight.—Males were heavier and larger than the females (Table 2). Nesting males and females were significantly heavier (one-tailed *t*-test Male, $t = 5.5$, $P < 0.005$, df = 237; Female, $t = 4.5$, $P < 0.005$, df = 274) than those captured in nonbreeding flocks. During the breeding season, body weight differed significantly among adult males ($F_{9,200} = 5.21$; $P < 0.0005$; df = 209) and adult females. There was an increase in the body weight of both sexes in December, at the end of the breeding season (Fig. 1). In November, males weighed an average (±SD) 50.1 g ± 1.8, N = 18 and in December they weighed 53.5 g ± 3.62, N = 10. The corresponding average mass for females was: November 46.1 g ± 4.1, N = 13 and December 53.7 g ± 3.88, N = 2. The body weight of both sexes decreased when the new reproductive cycle began in the month of January (Fig. 1). The variation in weight of both sexes was greater during the rainy season than dry season (one-tailed *t*-test: Male, $t = 3.89$, $P < 0.0005$, df = 193; Female, $t = 1.97$, $P < 0.02$, df = 252).

Molt.—I found individuals molting (body wing molt was simply recorded as present or absent) throughout the entire breeding season. Of

TABLE 2

MORPHOLOGICAL CHARACTERISTICS AND WEIGHT OF ADULT INDIVIDUALS WITHIN A POPULATION OF *COLUMBINA TALPACOTI*

Characteristics	Captured in flocks				Captured in nests			
	Adult female		Adult male		Adult female		Adult male	
	N	$\bar{x}$ SD	N	$\bar{x}$ SD	N	$\bar{x}$ SD	N	$\bar{x}$ SD
Weight (g)	247	46.0 ± 3.49	210	48.6 ± 3.73	27	49.5 ± 6.20	29	52.7 ± 3.70
Wing length (mm)	247	85.4 ± 2.63	210	87.5 ± 2.21	23	85.6 ± 2.40	29	88.8 ± 1.80
Tail length (mm)	247	64.0 ± 5.94	210	67.4 ± 3.93	25	66.4 ± 4.10	29	68.8 ± 3.20
Beak length (mm)	247	12.8 ± 0.49	210	12.8 ± 0.48	27	12.9 ± 0.28	29	13.0 ± 0.52
Beak width (mm)	220	6.0 ± 0.30	170	6.2 ± 0.27	23	6.3 ± 0.34	23	6.3 ± 0.39
Beak height (mm)	220	4.4 ± 0.28	170	4.4 ± 0.28	22	4.6 ± 0.51	23	4.4 ± 0.29
Tarsus length (mm)	220	15.3 ± 0.66	170	15.5 ± 0.63	23	15.0 ± 0.69	23	15.4 ± 0.55

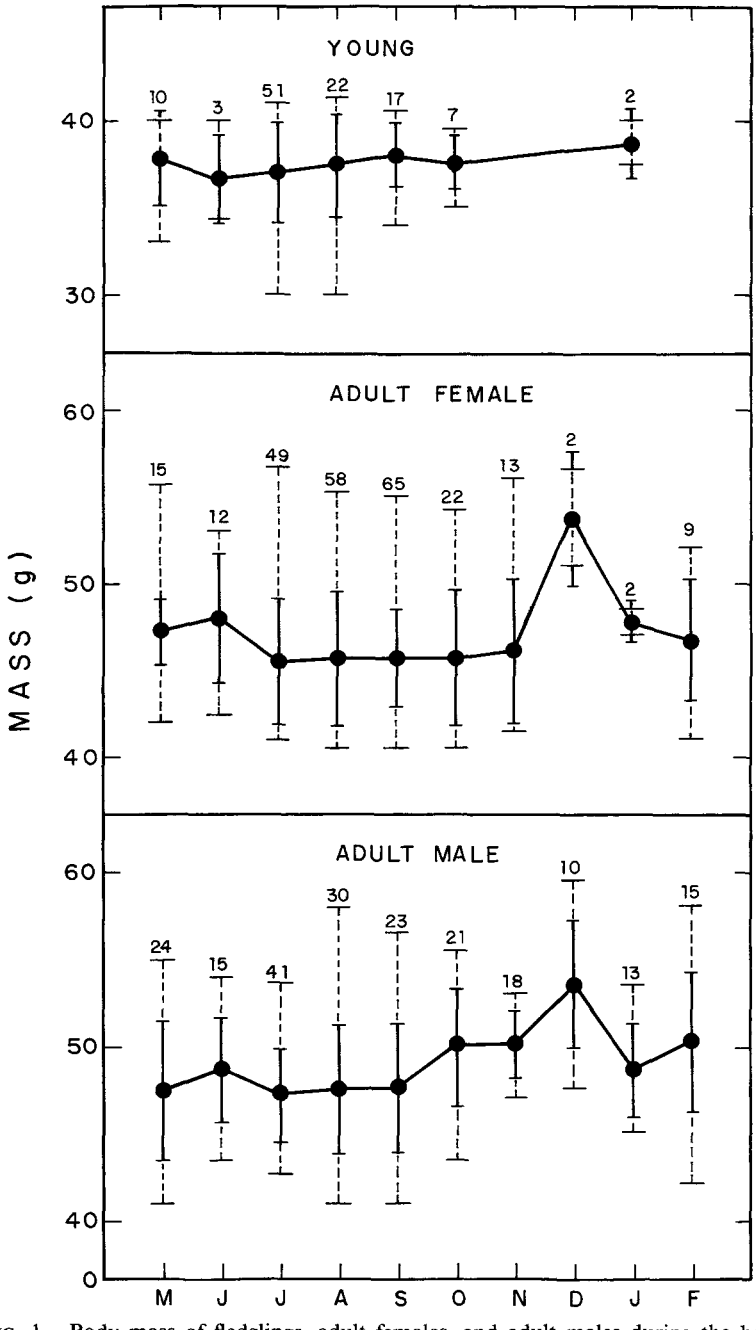

FIG. 1. Body mass of fledglings, adult females, and adult males during the breeding season of *Columbina talpacoti*.

the total 218 individuals observed, 79 (36.2%) were males in molt; 24 (11%) were males not in molt; 88 (40.4%) were females in molt and 27 (12.4%) were females not in molt.

Diet.—Ruddy Ground-Doves collect seeds from the soil by pecking and swallowing them rapidly. They are capable of eating seeds ranging in size from 2 mm in length (wild *Paspalum*) to corn seeds 15 mm in length. A qualitative and quantitative analysis of the crop content of 15 fledglings and 35 adults (found dead during this study) showed that the Ruddy Ground-Dove is a seed eater, although two snails and one insect were found. The same general diet has been reported by Trollope (1974) and Schubert et al. (1965). The introduced grass *Brachiaria plantaginea* and the wild native gramineae *Paspalum convexum* were the major food items (Cintra et al., unpubl. data).

Predation.—There were no significant differences (level of 5%) in either the spatial location or height between predated and undisturbed nests. The mean height in the tree for predated nests was 2.0 m ± 1.29, N = 60 and for intact nests was 1.96 m ± 1.35, N = 72, while the average distance of predated nests from the tip of the branch was 0.96 m ± 0.74, N = 56 and intact nests was 1.0 m ± 0.63, N = 71. On two occasions I observed Curl-crested Jays (*Cyanocorax cristatellus*) eating eggs and nestlings of Ruddy Ground-Doves. The American Kestrel (*Falco sparverius*), the Aplomado Falcon (*F. femoralis*) and an unidentified snake were also observed taking nestlings. The two falcon species cited above and the Roadside Hawk (*Buteo magnirostris*) were also seen capturing fledglings from Ruddy Ground-Dove flocks.

Reproductive dynamics.—Although the percentage of active nests showed little variation (between 3 and 14%) among months throughout the year (Fig. 2D), there was a peak in fledgling production in July (Fig. 2A). The percentage of active nests decreased in the last months of the year (Fig. 3) and increased again in January 1983. The percentage of eggs laid and chicks hatched followed the same pattern (Fig. 2B, C). Of the 422 eggs laid, 67.3% hatched with success and 32.7% were lost. Of those lost, 70.1% were predated, 13.9% were deserted, 13.1% were infertile, 0.7% were lost due to my interference (when adults were flushed from their nests) and 2.2% were lost for unknown reasons. The highest rates of egg predation occurred at the beginning and at the end of the breeding season (Fig. 3C). There was a significant difference in the rate of predation on eggs (χ^2 = 26.7; $P < 0.005$; df = 11) during the breeding season.

Parental desertion of eggs occurred in six months of the year with the highest percentage in September (Fig. 3B). Egg infertility also occurred in six months. The period of highest infertility was in January, at the be-

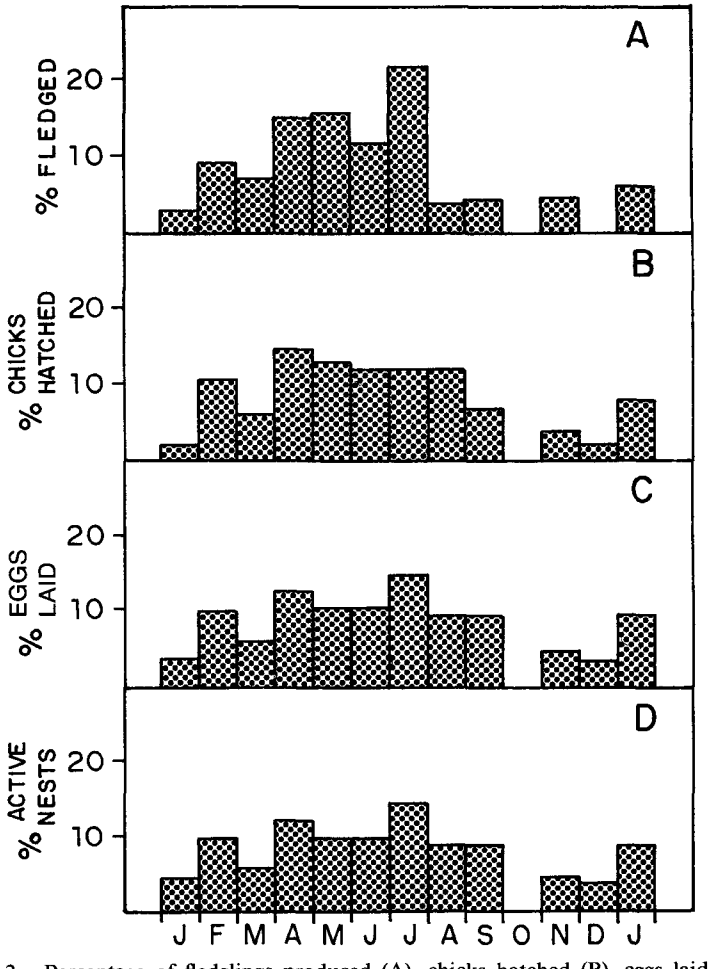

FIG. 2. Percentage of fledglings produced (A), chicks hatched (B), eggs laid (C) and active nests (D) throughout the year.

ginning of breeding season (Fig. 3A). Of 284 eggs that hatched, 37% of nestlings were lost. Of those, 75.0% were preyed upon in the nest, 10% were deserted and died, 7% died in the nest (probably due to rain) or fell from the nest, 3% died of disease, and 5% died for unknown reasons. The peak of hatchling predation occurred in August (Fig. 4D), in the month following peak fledgling production. There was a significant difference in the rate of nestling predation ($\chi^2 = 37.2$; $P < 0.005$; df = 10) during the breeding season. Parental desertion of nestlings occurred only between

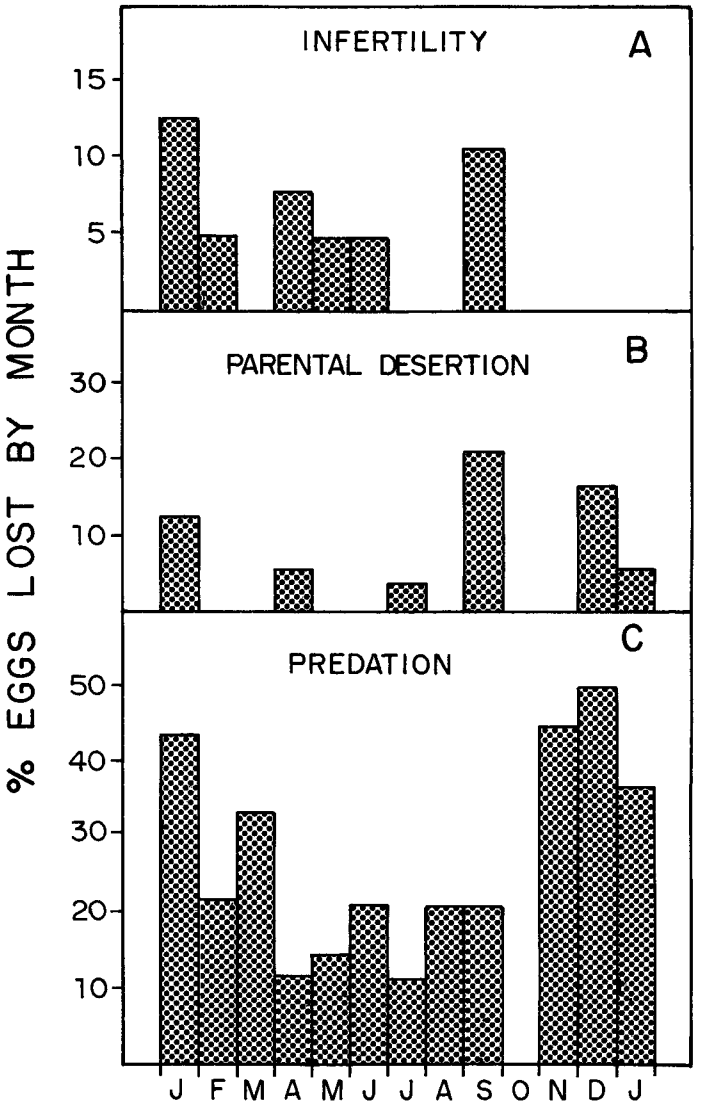

FIG. 3. Percentage of eggs lost during the breeding season of *Columbina talpacoti* due to infertility (A), parental desertion (B), or predation (C).

May and September (Fig. 4C). Nestling loss due to rain occurred in four months (Fig. 4B) but not at high rates. Similarly, loss due to disease was minor (Fig. 4A).

Reproductive success.—The method proposed by Mayfield (1961, 1975)

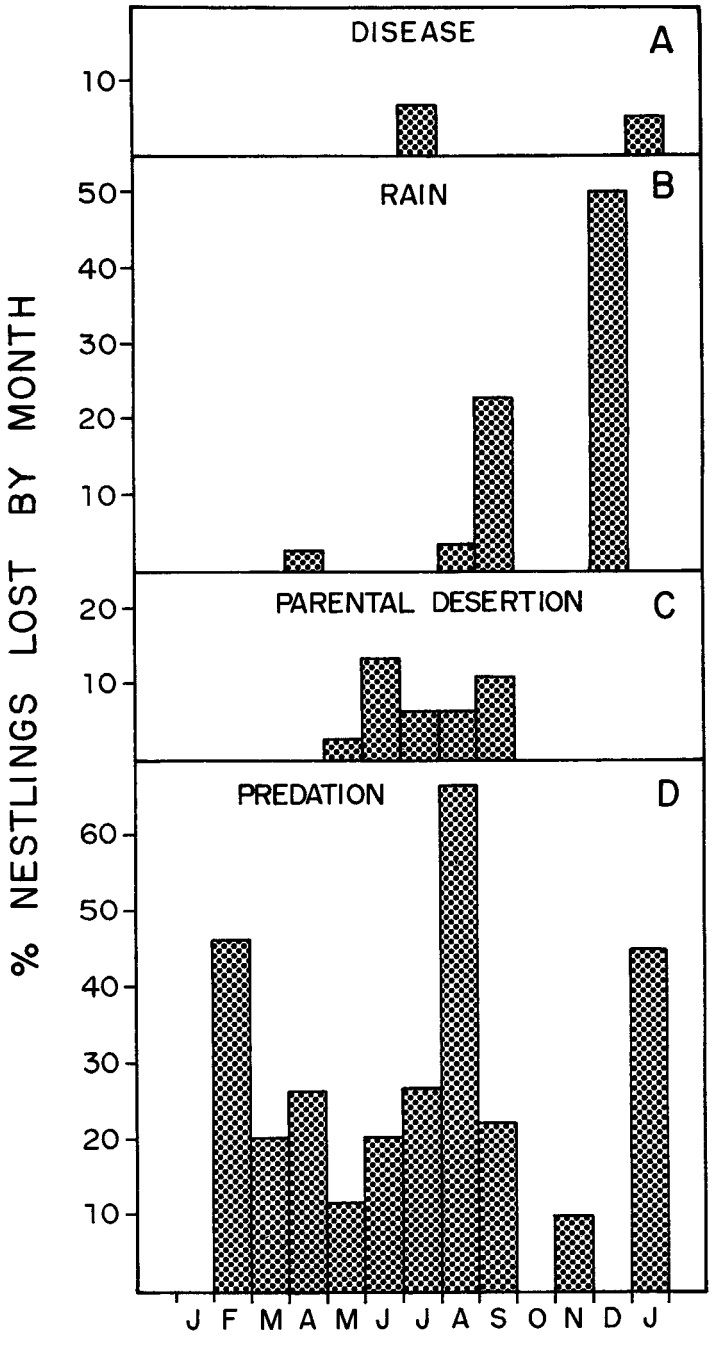

FIG. 4. Percentage of nestlings lost during the breeding season of *Columbina talpacoti* due to disease (A), rain (B), parental desertion (C), and predation (D).

is based on nest exposure to predators. The unit of exposure that I use here is the nest-day. I calculated daily mortality rates (m) for eggs and nestlings. The daily mortality rate (m) is Σ i (where i = 1 if the nest was predated and i = 0 if the nest was not predated) divided by Σ d (d = number of days that each nest was exposed to predation). The survival rate is consequently (1 − m) and the proportion of surviving nests after N days of exposure is $(1 - m)^N$. Hence the probabilities of survival based on nest exposure can be calculated given an incubation period of 12 days and nestling period of 11.8 days. Table 3 shows a daily mortality rate during incubation of 4.4% (daily survival rate of 95.6%) during 1982 and the first month of 1983, ranging from 2.6% in April–May to 8.3% in November–December. The incubation period is 12 days; so the probability of a nest remaining to hatching time is $(.956)^{12}$ or 58%. For nestlings the daily mortality rate during the same period was 3.8% and ranged from 1.1% in August–September and November–December to 5.6% in February–March. Thus the probability of a nestling remaining in the nest until fledgling is $(0.962)^{11.8}$ or 63.3%. Total nest success can be calculated by summing survival rates for the egg period and for the nestling period. By multiplying the probabilities of a nest surviving through each period we can calculate the probability of surviving from laying to fledging. In *C. talpacoti* it is 0.580 × 0.633 = 0.367 or 36.7%. I calculated that the mean number of young fledged per nest was 2.0 (mean clutch size) times 0.58 (probability of surviving through incubation), which equals 1.16 nestlings per nest at the end of incubation. Of these, 63.3% or 0.75 nestlings per nest can be expected to fledge.

DISCUSSION

Haverschmidt (1953) and Skutch (1956) reported that *Columbina talpacoti* nested throughout the year. It is advantageous for pairs to nest principally during the rainy season and the beginning of the dry season, because of the abundance of cultivated seeds during these times. The grass *Brachiaria plantaginea,* the principal food source of *Columbina talpacoti* (Cintra et al., unpubl. data), produces seeds from January to June (Filqueiras, pers. comm.). Thus there exists a relation between the time of egg laying and food resource abundance. Food availability probably was not a problem for this population, because during the study period I never found a nestling that died from starvation. This population of *C. talpacoti* nested near patches of *Brachiaria, Paspalum,* and other grains available from the farms.

Ninety percent of the nests were constructed in forks of horizontal limbs. This preference may be due to greater availability of horizontal limbs in the cypress than in the coffee trees. Four nests were built on the ground. This is the first record of ground nests for the species.

TABLE 3

VARIATION OF DAILY MORTALITY RATE FOR EGGS AND NESTLINGS OF THE RUDDY GROUND-DOVE BASED ON THE MAYFIELD METHOD

	Feb/Mar	Apr/May	Jun/Jul	Aug/Sep	Nov/Dec	Jan/83	Total
Mortality of eggs	0.031	0.026	0.028	0.058	0.083	0.034	0.044
	(34)[a]	(38)	(38)	(35)	(13)	(19)	(177)
Mortality of nestlings	0.056	0.020	0.026	0.010	0.010	0.045	0.038
	(23)	(36)	(40)	(24)	(09)	(12)	(144)
Probability of success[b]	0.34	0.57	0.52	0.43	0.31	0.38	0.36

[a] The numbers within parentheses correspond to sample sizes.

[b] $P = (1 \times m_{eggs})^I \times (1 - m_{nestlings})^N$. I = duration of incubation; N = duration of period with nestlings in nest; $(1 - m) = S$ = daily survival rate.

One adult always remained in the nest during incubation. I found no increase in intensity of intraspecific nest defense through the nesting cycle. Possibly my results were affected by sample size and the method that I used. Knight and Temple (1986) warned that "increased intensity of nest-defense behavior is largely a result of the methods used by the researchers." They suggested that repeated visits by observers modify the nest-defense behavior through positive reinforcement and loss of fear by nesting birds.

I found one male that reached sexual maturity in three months. This indicates that fledglings could be able to reproduce at the beginning of the following rainy season, or at the beginning of the next breeding season (January), when population density is low and there are fewer aggressive older individuals to inhibit nesting by younger birds.

Unfortunately, I observed parental care of only one pair after the young fledged. The two fledglings were fed by the parents until 25 days old.

Nesting adult males and females were significantly heavier than those in flocks. Possibly those adults that are reproducing are in better physical condition and/or are more mature than those in flocks. Individual weights of adult males and females differed significantly between wet and dry seasons. Murton et al. (1964) suggested that seasonal variation of body weight of adult doves could be adaptive because loss of body weight (and consequently loss of food reserves) occurs in the dry season when the balance between subsistence and resource level is critical. During the dry season, effects of environmental factors (such as low relative humidity, wind, and temperature) should result in a more intense water loss and, consequently, adult weight loss.

Some species of the predators (*Falco sparverius, F. femoralis*) also breed during the dry season, possibly as a result of the greater ease in finding their prey (cerrado vegetation is extremely dry in this period). As for young tropical birds, predation is the most important factor responsible for mortality of eggs and nestlings. Of the total dove eggs laid, 22.7% and 27.8% of the total number of nestlings hatched were destroyed by predators. These results are similar to those found by Skutch (1956) for *C. talpacoti* in Costa Rica. He found 24% nest success and 20% egg success. Carvalho (1957) found a slightly higher success rate in this species. Of 20 eggs, only 7 (35%) young fledged. In Surinam, Haverschmidt (1953) observed that in three clutches with a total of 5 young, all left the nests. In the present study there was significant seasonal variation in the rate of predation on eggs and on nestlings. Fledgling production and percent of nests predated both peaked in July indicating that predation may be density dependent.

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