

similar-sized boxes made a single layer with 3 or fewer young, but a double layer in larger brood sizes. In both species, the average weight of nestlings at age of effective homeothermy can be less in larger broods, even though age of effective thermoregulation remains about the same. The difference in behavior and nest construction might affect thermoregulatory abilities in hot weather, but this has not been tested in either species.

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**The Oilbirds of Los Tayos.**—A comprehensive investigation of the fauna of the Los Tayos caves (3° 06' S, 78° 12' W), in the Morana-Santiago Province of Ecuador, was one of the main objectives of the 1976 Ecuadorean-British Los Tayos Expedition. I studied the population of Oilbirds (*Steatornis caripensis*) inhabiting the caves.

The Los Tayos caves are situated in forested country at an elevation of 550 m in the eastern foothills of the Andes. The main entrances to the caves are 2 vertical shafts 55 m and 75 m deep and approximately 60 m apart. While the total cave system is large and complicated, with a surveyed length of 4900 m including several parallel systems, some with narrow exits, only the area within 200 m of the 2 main shafts was occupied by Oilbirds. The extent of the Oilbird's occupation was assessed by the position of the large deposits of seeds in the cave regurgitated by the birds after digestion of the pericarp.

*Size of the Los Tayos colony.*—The large size of the seed deposits, at least 2.5 m deep, indicated a long occupation by a large colony of Oilbirds, but relatively few of them (ca. 170) were in the caves during our visit. Indirect evidence of the probable size of the colony was obtained from local Indians. Traditionally these people harvest the young Oilbirds each year in April; in April 1976 they claim to have taken 500 young birds. A long-term investigation of the biology of the Oilbird in Trinidad (D. W. Snow, *Zoologica* 46:27–48, 1961; *Zoologica* 47:199–221, 1962) showed that on average a little over 2 young were reared per pair. If the nesting success at Los Tayos was similar then approximately 500 adults will have reared the 500 young birds killed. As many nesting ledges in the caves were very high and inaccessible to the Indians and annual harvesting of the young is a long cultural tradition, the proportion taken is likely to be a sustainable yield, indicating a total adult population of well over 500 birds, probably at least 1500.

On 14 July and 2 August between dusk and 21:00, I censused the Oilbirds as they left both vertical shafts of the cave to forage. On both evenings nearly all the Oilbirds left via the wider 75 m shaft. They negotiated the shaft singly using their echo-locating clicks as they circled upward. When they got out of the shaft they stopped echo-locating and flew into the forest. On 14 July 156 birds emerged and on 2 August 13 did so. On the former date after the main exodus a few adults could be heard still calling and clicking in the cave.

*Breeding, and post-breeding exodus.*—I entered the caves on 15, 20, and 24 July by means of a winch erected by the caving team. The occupied nesting ledges were all high and inaccessible, but from the cries of the young begging for food and from what I could view from below, I estimated that there were probably 10 to 15 nests with large young

TABLE 1  
WING LENGTHS AND WEIGHTS OF YOUNG OILBIRDS

Estimated age (days)	Wing (mm)	Weight (g)	Average wt. and range at equivalent age in Trinidad
100 <sup>1</sup>	279	281	485 (420-550)
80	200	196	600 (550-650)
80	244	165	600 (550-650)
60-70	125	228	520 (390-650)

<sup>1</sup> Fledged bird trapped in net.

on 15 July. By 24 July the cave appeared to be empty of Oilbirds except for 1 family of large young. During 4 July different young Oilbirds were picked up from the cave floor having fallen from the nests; all were emaciated. The weights and measurements of 3 of them, and of a fully fledged young bird caught on 7 July in a net 200 m from the shaft, are shown in Table 1.

Oilbirds in Trinidad take between 88 to 125 days to fledge; they reach a peak weight of ca. 650 g between 70 to 80 days, which then declines by approximately 200 g before fledging. Using the Trinidad data on wing length as a basis for estimating age, a comparison between the weights of the Los Tayos young and the young Trinidad birds is also shown in Table 1. The unfledged young were 56-72% below the weight of the Trinidad young and the fledged bird 42% below.

Between 7 and 25 July some members of the expedition were present in the Los Tayos caves each day but nobody actively disturbed the Oilbirds and it does not seem likely that human disturbance caused the exodus of most of the breeding population and the very low weights of the young.

If such a post-breeding exodus is normal it is in sharp contrast to the behavior of the Trinidad population which occupy their nesting ledges throughout the year. Huge numbers are also always present at the Caripe cave in Venezuela, now a national park and visited daily by tourists without disturbance to the birds.

*Food.*—The Oilbirds in Trinidad take their fruit almost entirely from 3 families and in the following proportions: Palmae 52%, Bursaceae 25%, and Lauraceae 23%. All these fruits have nonsucculent pericarps enclosing a single seed. Analysis of the pericarp of some fruits from each family showed them to be high in protein (9-14% dry wt.) and fat 24-44% dry wt.). Most of the fruits taken by the Oilbirds at Los Tayos were also from these 3 families (Table 2). The seeds of the fruits taken by the Oilbirds at Los Tayos that have not been previously illustrated in Snow (1962) are illustrated in Fig. 1 except for *Jessenia bataua* whose seed appears identical to *Jessenia oligocarpa* of Trinidad. A sample of all the Oilbird seeds from the Los Tayos cave has been preserved and is deposited at the Sub-department of Ornithology of the British Museum (Nat. Hist.) at Tring.

Only 1 palm (*Morenia caudata*) was found with ripe fruit that could be collected for analysis. Twelve of these fruits weighed 53.5 g of which 35.5 g was seed and 16.5 g (31%) pericarp. The pericarp of the 12 fruits dried in the field weighed 3.0 g. Analysis of this dried pericarp showed it to be 11% fat; 9% protein; 70% carbohydrate, ash and crude

TABLE 2  
PERCENTAGE PROPORTIONS OF OILBIRD FRUITS

	Random sample of seeds from top 30 cm of deposit	Freshly regurgitated seeds <sup>1</sup>		
		15 July	20 July	24 July
Burseraceae				
<i>Dacryodes</i> sp.	56	27	4	7
Palmae				
<i>Jessenia bataua</i>	3	—	2	—
<i>Euterpe</i> sp.	10	66	88	87
<i>Morenia caudata</i>	3	—	5	1
<i>Socratea</i> sp.	18	—	—	2
Lauraceae				
<i>Aniba</i> sp.	3	2	—	—
Small Lauraceae sp. (seed 15 × 9 mm)	2	—	—	—
Annonaceae sp.	4	—	—	½
Polygonaceae				
? <i>Coccoloba</i> sp.	2	4	1	2
Total seeds	460	48	193	187

<sup>1</sup> For sampling, I laid out a plastic sheet (183 × 274 cm) below some occupied ledges.

fibre; and 10% residual moisture. An analysis was made of the dried pericarp of 2 palm fruits taken by the Oilbirds in Trinidad; the results were *Bactris cuesa* protein 13%, fat 39%, *Jessenia oligocarpa* protein 5%, fat 26%, so both were considerably higher in fat than *Morenia caudata*.

Two methods were used to assess the fruit diet. A large random sample of seeds from the top 30 cm of the deposits was taken in the 2 largest colonies from dry areas. Some seeds, particularly the palms, are more durable than others so may be slightly over represented by this sampling method. Recently regurgitated seeds were also sampled. Before laying out a plastic sheet on 15 July to sample recently regurgitated seeds, the fresh seeds on the surface, identifiable by the pink or purplish stain made by the recently enclosing pericarp, were collected. A general search of the cave deposits did not produce any more kinds of seeds than were taken in the samples.

During the short span of observations the changes in the birds' diet suggested a food shortage. There was a decrease in the proportion of *Dacryodes*, a large fruit with a seed size averaging 26 × 17 × 16 mm; while the proportion of the palm *Euterpe* was high throughout July and increased in the second half. *Euterpe* has a round seed that varies in diameter from 9–16 mm (average of 12 seeds 13 mm) and is the smallest fruit taken by the Oilbirds at Los Tayos. The fresh *Euterpe* seeds collected were nearly all below average: of the 32 seeds collected on 15 July the largest was 11 mm; of the 147 seeds collected on 20 July all but 3 were under 12 mm; and of 125 seeds collected on 24 July all but 1 was under 11 mm.

The most striking difference between the Oilbird's diet in Trinidad and Los Tayos is

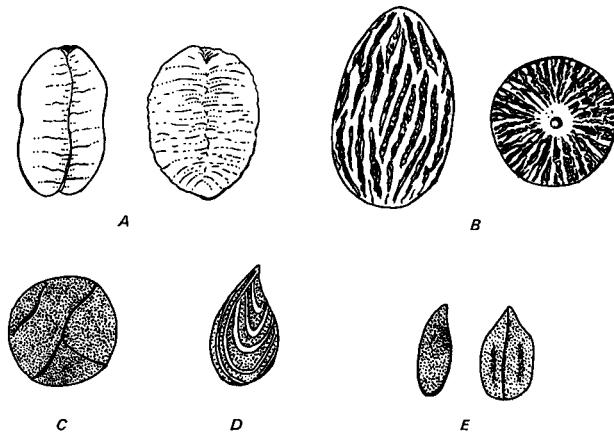


FIG. 1. Seeds of fruits eaten by Oilbirds. Natural size. A. Annonaceae sp., color reddish brown. B. *Socratea* sp., color reddish brown with black streaks. C. *Morenia caudata*, color black, indented lines. D. ?*Coccoloba* sp., color brown or black with raised fibres. E. Lauraceae sp., color dark brown.

the paucity of Lauraceae at Los Tayos. Two species of Lauraceae account for 5% of the large random sample taken at Los Tayos, compared to 15 species of Lauraceae accounting for 23% of all seed samples taken in Trinidad.

Yaupi caves, 33 km ENE of Los Tayos caves, were visited by some members of the expedition between 26 and 31 July. No Oilbirds were found in the caves but there were deposits of Oilbird seeds. The local Indians claim that Oilbirds breed there and they harvest the young in March and April. A. Hutson kindly collected a small sample of the seeds, picking out as many different kinds as he could find. This sample includes all the palm species shown in Table 2 but only 2 dicotyledon species, the Annonaceae species, and an unidentified species not found at Los Tayos. The absence of *Dacryodes* and of the Lauraceae is not surprising as Yaupi caves are below 275 m, where the Rio Santiago has left the mountains, and *Dacryodes* is a mountain species as are most of the Lauraceae.

*Comparison between Los Tayos and Trinidad colonies.*—The Oilbird colony studied at Spring Hill in Trinidad was a small one of 25 to 30 birds in a small partially roofed gorge and the size of the colony was almost certainly controlled by the number of suitable nesting ledges. Since the study was made the addition of a few artificial ledges has slightly increased the size of the colony. The cave is surrounded by rich forest and the nearest neighboring Oilbird cave is 8 km away. Throughout the 4½ years of the Trinidad study there was no indication of food shortage. The year-round occupation of nesting ledges here may be necessary to ensure the opportunity to breed.

At Los Tayos on the other hand, the colony size is probably not limited by available nesting ledges as much of the cave system is not used; therefore year-round occupation might serve no function. Colony size is possibly limited by the fruit available within the energetically economic foraging distance from the cave. If this is so it would not be surprising that at the end of the breeding season the young should be very much underweight or that the adults desert the cave at this time.

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**Observations on the nesting biology of the Great Cormorant in Ethiopia.**—The breeding biology of the Great Cormorant (*Phalacrocorax carbo*) is fairly well known for northern temperate populations (Cramp and Simmons, *Birds of the Western Palearctic* Vol. I, Oxford University Press, Oxford, 1977; Palmer, *Handbook of North American Birds* Vol. I, Yale University Press, New Haven, 1962) but not for African populations (Olver and Kuyper, *Ostrich* 49:25–30, 1978; Urban and Jefford, *Emu* 74 [Suppl.]: 294, 1975). This paper, one in a series on the breeding biology of large water birds nesting in the Rift Valley of Ethiopia, presents observations on breeding plumage, pair formation, nest building, incubation, and behavior, care and predators of nestlings of *P. c. lucidus*.

*Study area and methods.*—Observations were made at Lake Shala (7° 30' N, 38° 30' E; 330 km<sup>2</sup>; max. depth 266 m; pH 10.0) and Lake Abiata (7° 35' N, 38° 35' E; 196 km<sup>2</sup>; max. depth 14 m; pH 10.3) (Urban, *Ibis* 116:263–277, 1974). Throughout the period of observation from 1964–1974, the Great Cormorant nested at Shala on trees on islands, although in 1969–1974 they also nested at Abiata in trees surrounded by water due to a substantial rise in the lake's level. Observations, made usually once a month on weekends, totalled 240 h in 87 visits to Shala and 110 h in 56 visits to Abiata. The birds were observed from at least 20 m away in a boat or on the ground. No blind was used nor were any nestlings or adults banded or marked. Classification of *carbo* used in this paper is from Urban and Jefford (*Bull. Br. Ornithol. Club* 94:104–107, 1974); names of colors are from Palmer (op. cit.); and names of displays are from van Tets (*Ornithol. Monogr.* 2, 1965).

*Breeding plumage.*—The lores—orange in male and scarlet, scarlet-orange, or orange in the female early in the nesting cycle—turn orange-yellow in both sexes once incubation begins. The breeding plumage is otherwise essentially the same in both adult sexes: the cheeks, throat, and upper breast are white while the rest of the body is black glossed with olive. The lower breast and abdomen are speckled white and black in immatures (2- to 3-year-olds ?) and white in 1-year-olds. An oval white patch is often present (adults only ?) on either side of the rump in both sexes, not only in males as stated by Olver and Kuyper (op. cit.). The gular pouch, olive to dark olive early in the breeding season, becomes olive to buffy yellow in late stages of incubation. The iris is emerald.

*Pair formation.*—Nesting activity commences when a few to several hundred cormorants appear at the islands at Shala or on the partly submerged trees at Abiata. Occasionally 300 or more individuals swim in a group close to the islands of Shala for several h before moving onto them. Pair formation at Shala and Abiata appears to be much like pair formation in *carbo* populations in northern temperate regions as described by Cramp and Simmons (op. cit.). Thus, males establish nest-sites and advertise on them by wing-waving; they are silent when doing so. Based on 30 observations, the males waved the wings 1.8 times per sec and 11 times in a sequence before stopping. European and North American