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BREEDING BIOLOGY OF THE SCARLET IBIS ON CAJUAL ISLAND, NORTHERN BRAZIL

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Abstract.—The reproductive biology of the Scarlet Ibis (*Eudocimus ruber*) and White Ibis (*E. albus*) is well known from sites in North America, the Caribbean, and the Venezuelan llanos, but few data are available on the status or breeding patterns of the populations that inhabit South American mangroves. From 1992–1997, we monitored the status of a colony of *E. ruber* in an area of mangrove in northern Brazil. The breeding population numbered 2000–3400 pairs. We did not find any significant population fluctuations between years; apparently, most birds attempted to breed each year, in contrast with freshwater-breeding populations. Clutch size was 1.97 ± 0.17, lower than at more northern saltwater sites. The low variability of clutch size was surprising. Whole nest failure from catastrophic events such as storms, human predation, and nest desertion was responsible for most egg and nestling mortality. Partial mortality was rare. Singleton eggs and nestlings were frequently abandoned by adults following the loss of an egg or nestling. We conclude that this population pursued a strategy of brood survival rather than brood reduction which is usually observed in *Eudocimus*. This may have resulted from stable resource availability at this site. Given that northern populations often do not breed in unfavorable years, selection appears to have favored adult survival over reproductive capacity in this species. Human disturbance was intense, and it can threaten ibis populations both through direct predation and induction of nest desertion.

BIOLOGÍA REPRODUCTIVA DE LA POBLACIÓN DE *EUDOCIMUS RUBER* EN LA ISLA DE CAJUAL EN EL NORTE DE BRAZIL

Sinopsis.—La biología reproductiva de *Eudocimus ruber* y de *E. albus* es bien conocida en localidades de Norteamérica, el Caribe y los Llanos de Venezuela, pero existen pocos data disponibles sobre el status y los patrones de reproducción de las poblaciones que viven en manglares sudamericanos. Entre 1992 y 1997, estudiamos el status poblacional de una colonia de *E. ruber* en una región de manglar en el norte de Brasil; en 1995 registramos también el tamaño de puesta, la mortalidad de huevos y pollos (hasta los 20 días), y el fracaso de nidos enteros. La población reproductiva fue de 2000–3400 parejas. No fueron encontradas fluctuaciones poblacionales sistemáticas entre años, y la mayoría de las aves intentó reproducirse cada año, en contraste com lo observado en poblaciones que se reproducen en agua dulce. El tamaño de puesta fue 1.97±0.17, menor que en localidades costeras situadas más al norte. La pequeña variabilidad del tamaño de puesta es sorprendente. Los fracasos de nidos enteros debidos a eventos catastróficos como tempestades, predación humana y la deserción de nidos por los adultos, fueron las principales causas de mortalidad. La mortalidad parcial fue rara. Los huevos y pollos únicos fueron frecuentemente abandonados por los adultos después de

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la pérdida de un huevo o pollo, lo que es común en ciconiiformes, pero puesto que el tamaño de la nidada casi siempre fue dos, esto significa que las nidadas fueron, o criadas enteras, o abandonadas. Concluímos que esta población se ajustó más bien a una estrategia *brood survival*, que a la estrategia *brood reduction* más común en *Eudocimus*. Esto puede haber resultado de una disponibilidad de recursos estable en esta localidad. Dado que los poblaciones más norteñas no se reproducen en años desfavorables, la selección parece haber favorecido la supervivencia de los adultos sobre la capacidad reproductiva en esta especie. Las perturbaciones humanas fueron intensas, y pueden amenazar las poblaciones de corocoros, tanto a través de la predación directa, como induciendo a la deserción de los nidos.

The Scarlet Ibis (*Eudocimus ruber*) occurs in both saltwater (Spaans 1990) and freshwater (Ramo and Busto 1985, 1988; Brouwer and Van Wieringen 1990) ecosystems in South America. However, most studies of Scarlet Ibis in South America have focused on freshwater systems (Ramo and Busto 1985, 1998; Brouwer and Van Wieringen 1990); studies of coastal populations have reported only on the status or location of breeding populations (e.g., Morrison et al. 1986, Spaans 1990, Rodrigues and Fernandes 1994). This is unfortunate because there are often important differences in the ecology of ciconiiforms occupying freshwater and saltwater ecosystems (Bildstein et al. 1990b, Frederick et al. 1992, Hancock et al. 1992). Thus, more data are needed from mangrove ecosystems to understand the reproductive biology of Scarlet Ibis at coastal sites in South America.

Therefore, the objective of this study was describe the status and breeding biology of a population of Scarlet Ibis breeding on Cajual Island in the Gulf of Maranhão, Brazil (Rodrigues 1995). Specifically, we quantified the size of the adult population as well as clutch size and reproductive success. As clutch size and brood reduction patterns differed from those recorded in other populations, our data form the base for a discussion of the role of these parameters in the breeding strategy of the population. Our data will also serve as a basis for evaluating the conservation status of this population.

STUDY SITE

Cajual Island covers an area of about 6000 ha and is located in the Gulf of Maranhão (2°26′S, 44°30′W), a broad estuary formed by the confluence of the Itapecuru, Mearim, and Pindaré Rivers with the Atlantic Ocean (Fig. 1). The site is part of a major coastal formation characterized by a highly indented coastline, broad belts of mangrove vegetation up to several kilometers in width, and extensive intertidal mudflats with dense populations of crabs (principally *Uca* and *Ucides*; Ocypodidae). Maximum tidal amplitude in this area is 8.16 m (Mabesoone and Coutinho 1970).

The present study was focused on a colony of Scarlet Ibis located on the island's northern sector. The nests were built 5–12 m high in dense 10–15-m tall mangroves (*Avicennia germinans*). The colony was divided into a number of subcolonies (Fig. 1).

METHODS

Population status.—We censused the Scarlet Ibis breeding on Cajual Island yearly from 1992–1997. Rodrigues (1995) presented data for 1991.

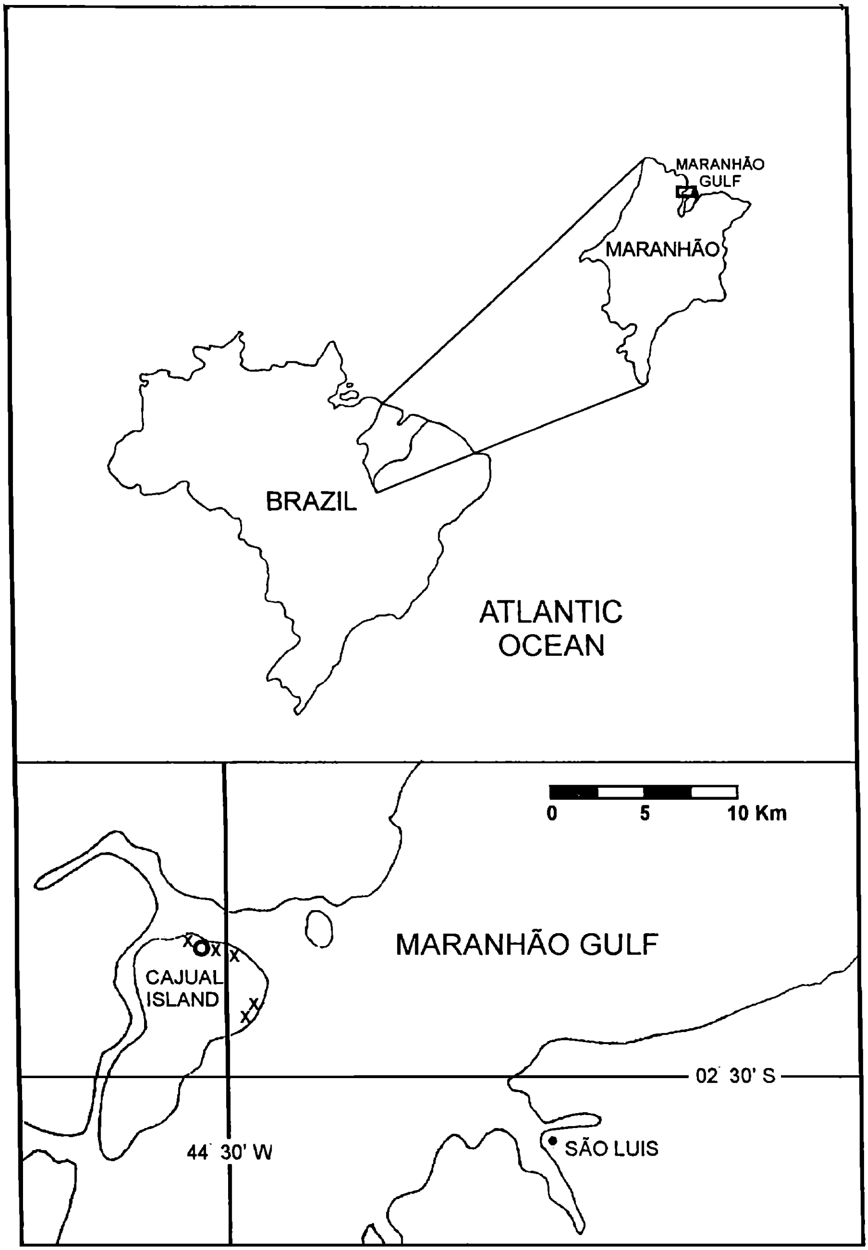

FIGURE 1. Cajual Island on the northern Brazilian coast. The open circle indicates the study site, crosses indicate other subcolonies.

The number of breeding pairs was estimated by counting all occupied nests in marked quadrats along parallel transects 50 m apart. Transects were censused by one observer just after high tide when adults were still present in the colony; an additional observer remained outside the colony to count adult birds in flight. Comparison between observer counts showed approximately 90% similarity. While replacement clutches were probably laid, and multiple clutches may occur, these phenomena were not considered in our estimates. During the 1996 breeding season (April–June), marked quadrat counts were compared with a more extensive count of the entire colony carried out by a single observer on foot. Even when censuses of the entire ibis population were not carried out, we made pre-breeding counts by boat.

Nesting biology.—We quantified nesting ecology in detail in 1995 in a portion of the colony containing 97 individually marked nests. We visited the colony twice each week from 19 July–6 September (laying through the first 20 d of life of the chicks) and counted eggs and/or chicks in each nest from an elevated position several meters from the nest. Each pair was disturbed only for a few minutes; we never remained in the colony for more than 2 h.

Total nest failure was differentiated from partial losses. As catastrophic losses were high, we estimated reproductive success using the apparent mortality method (Johnson and Schaffer 1990). Follow Mock and Parker's (1986) terminology, we refer to nests with a single nestling as B/1, and those with two nestlings as B/2. A "primary" B/1 brood is one that has contained a single nestling since hatching; a "secondary" B/1 brood previously contained more chicks.

Survival rates of broods of different sizes were not compared by the nest-case method because in the case of singletons, there is no difference between individual mortality and nest failure, distorting nest failure rates. Therefore, we studied the nestling case, estimating the probability of survival of primary B/1 and B/2 nestlings. Survival rates of B/1 and B/2 chicks were arranged in a contingency table and compared using *G*-tests (Sokal and Rohlf 1981). The same test was used to estimate differences in confidence limits between mortality rates of eggs and nestlings. We refer to mortality rates as the percentage of total mortality recorded during the given study period (incubation or nestling). All means are reported ± 1 SD.

RESULTS

Population status.—The breeding population on Cajual Island contained an estimated 2000 pairs in 1992, 2500 in 1993, 3000 in 1994, 3400 in 1996, and 2500 in 1997. Total adult birds in the area was approximately 6000–7500 in all years of the study.

Nesting biology.—Nesting phenology on Cajual Island was variable during the study period, with breeding occurring February–September (Fig. 2).

Mean clutch size was 1.97 ± 0.17 (n = 97); modal clutch size was 2 (94 of 97 nests). Of 191 eggs laid, 94 (49.2%) hatched; of 94 nestlings

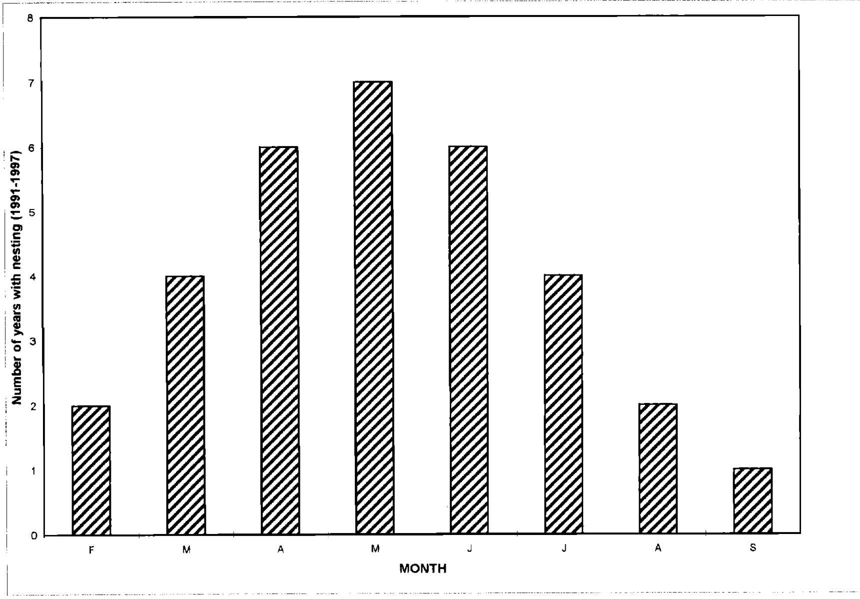

FIGURE 2. Scarlet Ibis breeding phenology on Cajual Island, 1991–1997.

hatched, 59 (62.8%) fledged. Mean net productivity per nest was 0.61 ± 0.90 chicks (59 fledglings from 97 nests).

Sixty-five (67%) of the 97 nests failed to produce fledglings. Total nest failure during incubation was recorded for 46 (47.4%) of the 97 monitored nests. Nineteen (37.3%) of the 51 nests still active at hatching also failed (Table 1). While failure was lower at the nestling stage, the difference was not significant (G = 1.4, df = 1, $P > 0.05$). Overall, 92.4% of deaths were due to nest failure; 7.6% occurred in successful nests (those fledging at least one young).

TABLE 1. Causes of nest failure in a sample of 97 Scarlet Ibis nests on Cajual Island, Brazil, 1995.

Cause of failure	*n*	% of total failures	% of failures with known causes
Desertion	8	12.31	27.59
Predation	9	13.85	31.03
Storms[a]	12	18.46	41.38
Unknown	36	55.38	—
Total failed nests	65	100.00	—

[a] Nests that disappeared immediately after storms. The ultimate causes could have been direct destruction by the storm or desertion by adults of damaged nests, and the latter having disappeared before our next visit. A nest was considered abandoned only when eggs or young were found cold or undernourished.

In those nests that hatched at least one egg ($n = 51$), a mean of 1.84 ± 0.36 eggs hatched. These nests originally contained 101 eggs, an egg mortality of 6.9%. An average of 1.84 ± 0.36 chicks fledged from successful nests ($n = 32$). These nests contained 62 chicks at hatching, a nestling mortality of 4.8%.

As single eggs were laid in only three nests, it was not possible to compare hatching rates between clutches of different size. Only one singleton egg hatched, and the nestling died during the first week. During the nestling stage, mortality was significantly lower ($G = 5.2$, df = 1, $P < 0.05$) in chicks from primary B/2 nests (33.2%, $n = 86$) in comparison with that of primary singletons (75.0%, $n = 8$).

Causes of mortality.—We were unable to identify the causes of failure for 36 (55.4%) of the 65 failed nests. Storms, predation, and desertion were each responsible for approximately one third of the remaining failures (Table 1), although in a number of cases evidence of more than one cause of failure was found during successive visits. Large numbers of human footprints were found on some visits to the colony. We also observed individuals of both *Milvago chimachima* and *Cathartes aura* feeding on ibis eggs.

DISCUSSION

Population status.—The Scarlet Ibis population at Cajual Island contained approximately 2000–3400 pairs during 1992–1997, and most individuals appeared to attempt reproduction at least once each season. This contrasts with the pattern for the closely related (or conspecific; Hancock et al. 1992). White Ibis (*E. albus*) at some sites in North America, where the bulk of the population may fail to nest in drought years (Bildstein et al. 1990a,b; Frederick 1990). Scarlet Ibis on Cajual Island feed their nestlings principally crabs (99.7% of the nestling diet; C. Martínez, unpubl. data). The consistent reproductive activity in all years at Cajual island may reflect a lack of dependence on freshwater lakes and swamps, whose annual fluctuations in water level result in drastic changes in prey availability. In contrast, Spaans (1990) found that Scarlet Ibises occupied colonies in mangroves irregularly in the region between the Orinoco and Amazon Rivers, and attributed this to among-year variation in some unidentified ecological condition. We suggest, however, that mangrove colonies might appear unoccupied in any given year if they are not monitored consistently because of the pronounced annual variability in nesting phenology (Fig. 2). Rodrigues and Fernandes's (1994) review of the literature also points to a highly variable breeding season in Brazil, a characteristic of tropical populations that would not be apparent from study of more temperate populations of *Eudocimus.*

Nesting biology.—On Cajual Island, modal clutch size was two, and no clutches had more than two eggs. This modal value persisted throughout brood development; mean brood sizes at hatching and at fledging were almost identical. Few nestlings in successful nests died. This pattern contrasts with other populations of *Eudocimus* (Kushlan 1977) and other ciconiiforms in which facultative brood reduction occurs (Fujioka 1985, Mock and Parker 1986, Mock and Ploger 1986). The mean clutch size of Scarlet Ibis at Cajual Island was smaller than that recorded at other sites, as might be expected given the latitudinal gradient described for other bird species, and the smaller clutch size recorded for coastal *Eudocimus* populations by Hancock et al. (1992). Variability in clutch size was also low at Cajual (cf. Kushlan 1977, Busto and Ramo 1982).

We might ask why no clutches with three eggs were observed. A stable resource base at Cajual may promote a relatively invariable clutch size. Resource predictability is probably also related to ciconiiforms preference for coastal colonies (Bildstein et al. 1990b, Frederick et al. 1992). Given that chicks at Cajual hatch and develop without any significant asynchrony (pers. obs.), and that more than 95% of hatchlings in successful nests fledged, the Cajual population fits the definition of a brood-survival strategist (Mock and Forbes 1994). This contrasts with many other ciconiiform populations, which are brood-reduction strategists.

Mock and Forbes (1994) argued that clutch size and brood reduction can only be fully understood when life-history selective consequences are taken into account. Adult survival is more important in long-lived birds. Even in the very different case of the colonies studied by Bildstein et al. (1990a), a substantial part of the adult population did not breed during bad years. This may reflect a selective priority for adult survival when breeding conditions are unfavorable. Despite the fact that most adults at Cajual attempted to breed, the fact that no more eggs were laid than the adults were able to rear indicates a relatively small investment in each successive breeding attempt. As Mock and Forbes (1994) argued, the brood-survival strategy tends to be more advantageous when the proportion of good years in an adult's life is large. The number of bad years is probably relatively low in mangroves, where Scarlet Ibis use marine resources almost exclusively.

Egg and nestling mortality in our population was high, and was mainly attributable to failure of entire nests, both during incubation and nestling development. These results are also consistent with other studies (e.g., Frederick and Collopy 1989a,b; Bildstein et al. 1990a,b; Brouwer and Van Wieringen 1990). Partial evidence indicates that catastrophic events, such as storms and human depredation, may have been the main causes of failure on Cajual. In a North American population of White Ibis (Frederick and Collopy 1989b), nest desertion accounted for 70.3% of total nest failures and 90.2% of failures of known cause (desertion in this case included storm-related disappearances and clutches found cold). On Cajual, the main cause of nest desertion would appear to be different, especially as storms destroyed nests directly, rather than inducing their desertion. The only common tendency in the two studies is for the ibises to abandon nests readily.

Although Scarlet Ibises on Cajual Island initiating breeding annually and appear to enjoy substantial reproductive success, human pressure in coastal habitats may disturb this equilibrium and threaten populations, both through nest depredation and induction of nest desertions. The current large population of Scarlet Ibis is not a guarantee of survival. In southern Brazil, where the species was once common, the Scarlet Ibis is practically extinct (Marcondes-Machado and Monteiro Filho 1989). Prevention of colony disturbance by humans must be given the highest priority, both at Cajual and at other sites in Maranhão, where human disturbance is general.

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