

NEST PREDATION IN RELATION TO NEST PLACEMENT IN THE GREATER ANI (*CROTOPHAGA MAJOR*)

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INTRODUCTION

Selection of a suitable nesting site may determine failure or success of the breeding attempt. For instance, nest placement affects the radiative environment and thus survival of eggs and nestlings (Walsberg 1981). Nest placement also affects the likelihood of predation upon eggs and nestlings (e.g., Robertson 1973, Robinson 1985, Strahl 1988, Götmark & Achlund 1988, Møller 1991, Storch 1991, Picman *et al.* 1993).

We studied the nesting behavior of the Greater Ani (*Crotophaga major*) in Venezuela, particularly the relationship between nest-site selection and nest predation. We found that nest survival depends on nest placement and argue that safety of the nest from predators might influence habitat selection in this species.

STUDY AREA AND METHODS

The study was carried out in “Hato Masaguaral”, a cattle ranch in Guárico state in

the central Llanos of Venezuela (8°34'N, 67°35'W). Vegetation ranges from open palm savannah in the west to dense gallery forest in the east, along the Guárico river and its tributary Caracol Creek. Scattered throughout the savannah are isolated patches of open woodland and shrubs (Troth 1979). Rainfall averages 1400–1500 mm annually, and is largely concentrated in May to November (Troth 1979), when Greater Anis nest (Lau 1987).

The Greater Ani, like its congeners, is a communal breeder (Davis 1941, 1942; Lau 1987). It is restricted to riparian vegetation along the borders of rivers, swamps, lakes, and streams with low, partly inundated banks (Davis 1941, Hilty & Brown 1986, Lau 1987). Along Caracol Creek groups of Greater Anis behaved aggressively towards each other, seemingly defending territories where single nests were built by each group. Between May and November 1986, we found 27 nests of Greater Anis along approximately 1.5 km of the flooded margins of the Creek, by observing the behavior of parents or by searching the vegetation. Nests were always built above

TABLE 1. Estimated nest survival¹ of Greater Anis in relation to nest placement in the Llanos of Venezuela.

Category	Nest placement	
	isolated	non-isolated
Daily survival probability of nest through egg period	1.000	0.941
Daily survival probability of nest through nestling period	1.000	1.000
Expected probability that nest survives through egg period	1.000	0.340
Expected probability that nest survives through nestling period	1.000	1.000

¹Probabilities calculated by the method in Mayfield (1975).

water. We measured its height and recorded, at 3–4-day intervals, the number of eggs or nestlings present. We marked eggs individually and recorded their hatching date to estimate fledging date for each nestling. We banded 3–5-day-old nestlings with unique color combinations to identify them individually. A nest was considered depredated if all eggs or chicks disappeared between two consecutive visits before their estimated fledging date. There was little uncertainty in determining whether nestlings had left the nest or had been depredated, because banded fledglings remained near the nest for several days after departure from the nest. A nest was considered successful if at least one nestling left it. We did not consider partial egg losses as depredated. Although some of these losses could have been due to predators, we could not distinguish them from losses caused by female tossing each others eggs from the nest (pers. observ.; see also Davis 1940, Skutch 1959, 1985, Vehrencamp 1977).

We found 12 nests before clutch completion, 9 after completion, and 6 after young had hatched. We assigned each nest to one of two categories of placement. Nests were considered “isolated” when supporting vegetation was completely surrounded by water and at least 1 m from adjacent vegetation. Such “islands” could be formed by shrubs, trees or

both. When these criteria were not met, nests were considered to be “non-isolated”. We did not measure other variables related to vegetation structure, but aspect of the vegetation seemed to be similar in every other respects in both patch types. Survival probabilities of nests, eggs and young in each nest group were calculated following the method in Mayfield (1975). We considered the egg period from the laying of the first egg to the hatching of the last young. We compared survival probabilities, number of young fledged, and nest height of the two groups of nests. Two nests could not be visited at the end of the estimated fledging period and the fate of those nestlings was unknown; therefore these nests were excluded from the survival analysis.

RESULTS

Nine of 25 nests (36%) failed to produce at least one young. All these total losses occurred during incubation and none during the nestling period. Nearly half (12) of the nests were built on “islands”, and these nests had a higher daily survival probability through the egg period (Table 1). Thus, nest survival through the egg stage was dependent on nest placement. (Fisher exact test, $P < 0.0001$, $n = 25$). In contrast, daily nest survival probability

through the nestling stage was similar of nest for isolated and non-isolated nests (Table 1).

When also considering partial losses (in addition to total losses), the mean proportion of eggs hatching per nest was significantly higher in isolated nests (Mean = 0.94, SD = 0.08, $n = 9$) than in non-isolated nests (Mean = 0.27, SD = 0.40, $n = 9$; Mann-Whitney test on arcsin-square root transformed data; $U = 74.5$; $P = 0.002$). In contrast, the mean proportion of nestlings fledgling per nest (considering total and partial losses), was similar for isolated and non-isolated nests (Mann-Whitney test on arcsin-square root transformed data; $U = 15$, $n_1 = 3$, $n_2 = 7$, $P = 0.301$). However, since only three non-isolated nests survived through the nestling stage, it is difficult to reach a firm conclusion.

As a consequence of the large differences in egg survival, a significantly greater number of young departed from isolated nests (Mean = 4.8, SD = 1.5, $n = 12$), than from non-isolated nests (Mean = 1.3, SD = 2.3, $n = 13$; Mann-Whitney $U = 15.5$, $P < 0.001$). Clutch size for nests found before clutch completion was similar in isolated and non-isolated nests (overall Mean = 7.6, SD = 1, $n = 7$).

Isolated nests were built significantly higher above the water (Mean = 2.2 m, SD = 1.1 m, $n = 11$), than nests in non-isolated areas (Mean = 1.1, SD = 0.2 m, $n = 10$; Mann-Whitney $U = 13.0$, $P < 0.005$). Height placement of non-isolated nests did not differ between successful (Mean = 0.95, SD = 0.11 m, $n = 4$), and depredated nests (Mean = 1.20, SD = 0.19 m, $n = 6$; Mann-Whitney $U = 21$, $P = 0.052$).

DISCUSSION

Breeding success of Greater Anis was related to nest placement. Success of nests placed on isolated patches of vegetation was approximately three times that of nests placed on

non-isolated sites because of predation during the egg stage.

Lower rates of predation on nestlings than on eggs of isolated, as well as non-isolated nests, could be explained by at least four non-exclusive reasons. First, anis were seen defending nests against potential predators (avian raptors and humans) only after eggs hatched. Second, nestlings Greater Anis have a very precocial and peculiar predator escape behavior, to some extent, similar to that of nestling Hoatzins (*Opisthocomus hoazin*, Strahl 1988). When disturbed, nestlings five-day-old and older are able to jump from the nest into the water below, and swim vigorously on the surface for up to several meters. Upon reaching the shore, they run on the ground and then become stationary, concealed in the vegetation for several minutes, before climbing back to their nests (Lau unpubl. data). This antipredator behavior should enhance survival probability of nestlings. Third, when handled, nestlings expel large quantities of a dense fluid through the cloaca that has an intense and repulsive odor that may act as a predator deterrent. It is possible that this substance has a glandular component since *Crotophaga* is known to have very large and structurally unique anal glands (Quay 1967). Finally, the total length of time that eggs are exposed to predators is considerably longer (approximately 20 days), than that of fledglings (approximately 8 days; Lau 1987). A short nestling period might be an adaptation to reduce predation in the nest, such as has been proposed for Pheasant Coucals (*Centropus phasianinus*, Taplin & Beurteaux 1992) that also leave the nest with a body mass considerably (c. 40%) below that of the adult.

The most likely predators in Caracol Creek were wedge-capped capuchin monkeys (*Cebus olivaceus*) and unidentified rodents (pers. observ., see also Strahl 1988). Troops of capuchins were frequently seen eating the eggs of Yellow-crowned Night-Herons (*Nycticorax nycticorax*).

corax violaceus) and Hoatzins. Capuchins do not swim across water barriers and therefore isolation from surrounding vegetation by water afford protection from this predator. Avian raptors were probably not important nest predators because they should not be affected by nest isolation. In addition, groups of Greater Anis were seen to successfully drive away Snail Kites (*Rostrhamus sociabilis*) and Black-collared Hawks (*Busarellus nigricollis*).

In two other Neotropical species of birds, isolation offers considerable protection against arboreal mammalian predators such as primates. In Amazonian Peru, island colonies of Yellow-rumped Cacique (*Cacicus cela*) have a significantly higher percentage of successful nests than colonies not isolated by water (Robinson 1985). Similar effects of isolation on nest survival have been found in Hoatzins nesting along the margins of Caracol Creek, our same study area, in Venezuela (Strahl 1988). In both studies, nest predation was mainly attributable to *Cebus* monkeys.

Contrary to some marsh nesting species, such as blackbirds, that prey extensively on insects that undergo aquatic stages (Orians 1980), Greater Anis use this kind of prey only in a small proportion. During 5 hours of observation at 2 nests we observed 40 nestling feeding events; 97.5% arthropod prey fed to the nestlings belonged to taxa that are exclusively terrestrial (Orthoptera 55%, Lepidoptera caterpillars 17%, spiders 8%, and 17.5% included Mantidae, Hemiptera, adults of Lepidoptera and Coleoptera), and only 2.5% of the prey were Odonata, that have aquatic nymphs. The lack of dependance on aquatic arthropods for nestling food, supports the idea that the close association of Greater Anis with flooded and riverine habitats may be a consequence of their preference for habitats that offer safer nesting sites. More generally, predation might be an alternative to competition and food limitation in

explaining the patterns of habitat selection in birds (Martin 1988, 1993; Picman *et al.* 1993).

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