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VIDEOGRAPHY OF PANAMA BIRD NESTS SHOWS SNAKES ARE PRINCIPAL PREDATORS

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Resumen. – Video documentación de nidos de aves de Panamá indica que las serpientes son los principales depredadores. – Utilizamos grabadoras de video para monitorear los nidos de dos especies de hormigueros en la Isla Barro Colorado, Panamá. Monitoreamos siete nidos del Hormiguero collarejo (*Hylophylax naevioides*), de los cuales sólo fracasaron cuatro, y nueve nidos del Homiguero dorsicastaño (*Myrmeciza exsul*), de los cuales ninguno resultó con éxtito.. Observamos 10 eventos de depredación, uno por el mono cariblanco (*Cebus capucinus*), uno por el coatí (*Nasua americana*) y ocho ocasionados por la serpiente *Pseustes poecilinotus* (Colubridae). Se observó una depredación parcial, en donde una serpiente ingirió un pichón y luego regresó al día siguiente para cazar el último pichón. Ninguno de los nidos resultó destruido, a excepción del nido depredado por el coatí. Encontramos que las serpientes predominan como depredadores mientras que, en observaciones anteriores, las aves se consideraban como los principales depredadores en el borde del bosque. El alto porcentaje de nidos depredados por serpientes, también es inconsistente con la hipótesis de que las altas poblaciones de mamíferos en la Isla Barro Colorado suele ser la causa de la alta taza de depredación de nidos y de la extinción de las especies de aves del sotobosque.

Abstract. – We used video recorders to monitor antbird nests on Barro Colorado Island, Panama. We monitored seven Spotted Antbird (*Hylophylax naevioides*) nests, of which four failed, and nine Chestnut-backed Antbird (*Myrmeciza exsul*) nests, all of which failed. We recorded 10 predation events, including single instances of predation by white-faced capuchin (*Cebus capucinus*) and white-nosed coati (*Nasua americana*). The most common predator was *Pseustes poecilinotus*, a colubrid snake, which accounted for all other predations. Partial predation occurred in one case where a snake took one nestling then returned the next day to consume the remaining one. All nests except the one depredated by coatis appeared undisturbed. The predominance of snakes as predators contrasts strongly with anecdotal observations made from nearby edge habitats where birds were the primary nest predators. Furthermore, the high percentage of nests lost to snakes is inconsistent with the hypothesis that unusually high mammal populations on Barro Colorado Island are responsible for high levels of nest predation and local extinctions of understory bird species. *Accepted 28 January 2005.*

Key words: Barro Colorado Island, bird nest predation, *Hylophylax, Myrmeciza,* Panama, predators, *Pseustes.*

INTRODUCTION

Nest predation is the primary cause of reproductive failure in most birds (Ricklefs 1969, Newton 1998). Avian ecologists have made great strides in recent decades toward measuring rates of nest failure for a wide variety of species, even gathering observations of nests across entire landscapes (Robinson *et al.* 1995).We have developed refined analytical methods aimed at detailed scrutiny of nest predation data (Mayfield 1975, Dinsmore *et al.* 2002, Shaffer 2004). Yet, we have rarely been able to identify and quantify the importance of specific predators at bird nests (Moore & Robinson 2004). The lack of such critical data is largely due to the brevity of predation events. Without continual nest monitoring, few predation events are witnessed and indirect methods, such as inspection of nest and eggshell remnants, lead to inaccurate inference of predator identity (Larivière 1999, Pietz & Granfors 2000). Only with the recent availability of time lapse video has our ability to identify predators at bird nests increased (Thompson *et al.* 1999).

Despite great interest in video recording, the technology still has two major drawbacks. It is costly in terms of both time and money (Thompson *et al.* 1999, Stake & Cimprich 2003). Consequently, identities of nest predators are still rarely known, even from well-studied bird communities. To our knowledge, no video identification of predators has been accomplished in Neotropical bird communities. Given that nest predation has been hypothesized to drive evolution of many life history traits in tropical birds, such as reduced clutch size and higher annual adult survivorship (Martin 1996, Robinson *et al.* 2000b), identification of predators is an important information gap in avian ecological studies. Heretofore, only anecdotal observations of predators at tropical bird nests have been accumulated (Skutch 1960, 1971; Sieving 1992, Robinson & Robinson 2001).

The wider ecological relevance of our study involves evaluations of hypotheses for bird extinctions on Barro Colorado Island, Panama. Barro Colorado Island has been used as a textbook example for how isolation and small island area lead to disintegration of animal communities over time (Meffe & Carroll 1994). The island has lost 35% of the breeding bird species found there 85 years ago when the former hilltop was isolated from nearby mainland forest during creation of Gatun Lake (Robinson 1999). Mesopredator release, the food web change where loss of the top trophic level, in this case large and wide-ranging cats, leads to the explosion in numbers of their middle-sized mammalian prey, has been the primary explanation for bird extinctions (Terborgh 1974, Sieving 1992). A key and as yet untested assumption of that hypothesis is that middle-sized mammals are responsible for most songbird nest losses.

Our main objective was to use continuous video monitoring to identify predators at understory bird nests on Barro Colorado Island. We also assessed the time of day at which predation occurred, whether or not nests were more susceptible to predation during the incubation or nestling phases, and the success of nest defense at thwarting predation attempts. Finally, we evaluated potential effects of video monitoring on fates of nests by comparing predation of video-monitored nests with those monitored following standard observational techniques.

METHODS

We searched for nests of Chestnut-backed Antbirds (*Myrmeciza exsul*) and Spotted Antbirds (*Hylophylax naevioides*) in the forest understory of Barro Colorado Island, Republic of Panama. Barro Colorado Island is a 1562-ha former hilltop covered in tropical moist forest and now isolated by the waters of Lake Gatun. Antbirds breed primarily from May to December during the annual rainy season (Willis 1974, Windsor 1990). The forest on the western half of the island, where we made our observations, is at least 400 years old (Willis 1974).

All nests were found and monitored following methods described in Robinson *et al.* (2000). We studied Chestnut-backed and Spotted antbirds because their island abundances are high (Robinson 2001) and nests are easily located in the forest understory. Chestnut-backed Antbirds place their open-cup nests on the ground, often at the base of a small plant or under cover of a fallen tree branch (Willis & Oniki 1972). Spotted Antbirds weave an open-cup nest into a forked branch of a small sapling; most nests are about 1 m above the ground (Willis 1972). We also monitored one nest of Slaty Antshrike (*Thamnophilus atrinucha*) which builds an open-cup nest 1 to 5 m above ground (Roper & Goldstein 1997).

Once we located an active nest, we placed a video camera nearby to continuously record activities until the nest fledged or failed. We used 3 camera systems (Furhman Diversified, Inc., Seabrook, Texas) which are described in detail by Thompson et al. (1999). Each system consisted of a small video camera (fitting in a 32 x 32 x 60 mm housing) equipped with infrared light-emitting diodes, attached by an 18-m cable to a weatherproof case housing a video recorder. The recorder was powered by a 12-Volt battery. The tiny video camera was held by an articulated and camouflaged arm mounted within 3 m of each nest. Recording speed was set at six frames per second so that we could record for 24 h on a standard T120 VHS videotape. Initial placement of the cameras required less than 20 min and subsequent daily visits to replace the battery and tape required an average of only 5 min. Since the recorder was located 15 to 18 m away from the nests, we did not visit nests each day unless an absence of bird activity suggested the nest had failed.

After predation, we reviewed the last tape to identify predators and the date and time at which predation occurred. In cases of partial predation, we considered each event a separate predation when the events appeared to be carried out by different individual predators. Individual snakes were identifiable by their variable dorsal patterns.

We measured possible disturbance caused by camera placement to antbirds by recording the length of time between camera placement and return of an adult to incubate, brood, or feed nestlings to the nearest minute. To compare return times between nests with eggs and nestlings, we used a Wilcoxon-Mann-Whitney U test. We also evaluated possible effects of cameras on risk of nest predation. Cameras could increase predation if human activities near the nest or the presence of cameras attract attention of predators. Cameras could also decrease predation if predators avoid nests with cameras because of human activities or the presence of surveillance equipment. We compared the predation rates of nests on Barro Colorado Island monitored by our video cameras with nests of the same species that never had cameras. The latter were visited once every 3 days to determine success or failure following standard procedures (Robinson *et al.* 2000).

The total number of nests we monitored was below the minimum sample size recommended for comparisons of nest predation rates with program CONTRAST (Sauer & Williams 1989), so we compared predation at nests with and without cameras by randomization procedures (Good 2001). We created simulated distributions of daily predation rates for each species. We randomly selected (without replacement) the number of nests observed by cameras from the distribution of nest exposure days. We then summed the exposure days for each randomly selected set of nests and divided that sum into the number of predation events at nests with cameras, then subtracted that quotient from one to obtain a daily predation rate. We repeated the procedure 1000 times for each species using Resampling Stats (Resampling Stats 2.0). We then used the resulting distribution to create

TABLE 1. Fates of nests monitored by videography on Barro Colorado Island, Panama.

Nest fate[1]	Chestnut-backed Antbird	Spotted Antbird	Slaty Antshrike	Total
Monkey	1	0	0	1
Coatis	1	0	0	1
Snakes	6	2	0	8
Weather	1	0	1	2
Censored	0	4	0	4
Successful	0	1	0	1
Total	9	7	1	17

[1]Depredated by white-faced capuchin, white-nosed coati or Neotropical bird snake; abandoned because of weather, censored because of camera malfunction or re-location, or successfully fledged young.

95% confidence intervals and to quantify the probability of obtaining measurement equal to or more extreme than those measured at nests with cameras.

RESULTS

We video-monitored 17 nests of antbird species between 30 April and 25 July 2001 (Table 1). Chestnut-backed Antbird nests were monitored for one to 10 days during incubation (N = 7) and 3 to 7 days during the nestling phase (N = 2). None of the Chestnut-backed Antbird nests fledged young. Eight nests were depredated and one was abandoned after a rainstorm flooded the nest during incubation. Spotted Antbird nests were more successful with at least one nest fledging young. Two depredated nests survived 6 and 22 days, respectively. Video samples of four Spotted Antbird nests were censored [camera system failed (N = 1), or were removed, (N = 3, 2 of which were later lost to predation)]. One nest of Slaty Antshrike was abandoned after the branch supporting the nest broke following a rain storm.

We recorded 10 predation events at Chestnut-backed Antbird (N = 8) and Spotted Antbird (N = 2) nests (Fig. 1). Snakes were responsible for eight predation events. All snakes were identified as the Neotropical bird snake (*Pseustes poecilonotus*), a diurnally foraging species common in central Panama (A. S. Rand pers. com.). All but two of the snakes were juveniles as judged by their age-specific markings and size. Partial predation occurred in one of the ten events when a snake ate one Chestnut-backed Antbird nestling on 4 July at 16:31, then returned and ate the second nestling on 5 July at 18:52.

Mammalian predators accounted for the other two predations. One white-faced capuchin monkey (*Cebus capucinus*) depredated a Chestnut-backed Antbird nest on the ground (Fig. 1C). White-nosed coatis (*Nasua narica*) depredated another Chestnut-backed Antbird nest when a group of females passed by the nest and one individual found the nest and consumed its two eggs (Fig. 1 B). A third incident involving a mammal was not a predation event, but included a pair of ocelots (*Felis pardalis*) disturbing the camera system as it recorded a Slaty Antshrike nest. The nest had been abandoned the day prior because the branch supporting the nest had broken during a rainstorm. The eggs remained in the nest, however, so we continued filming to confirm the nest was abandoned. At about 03:00, the two ocelots came into contact with the camera and knocked it over. They actively manipulated the camera for about 45 s before leaving the area. The ocelots did not consume

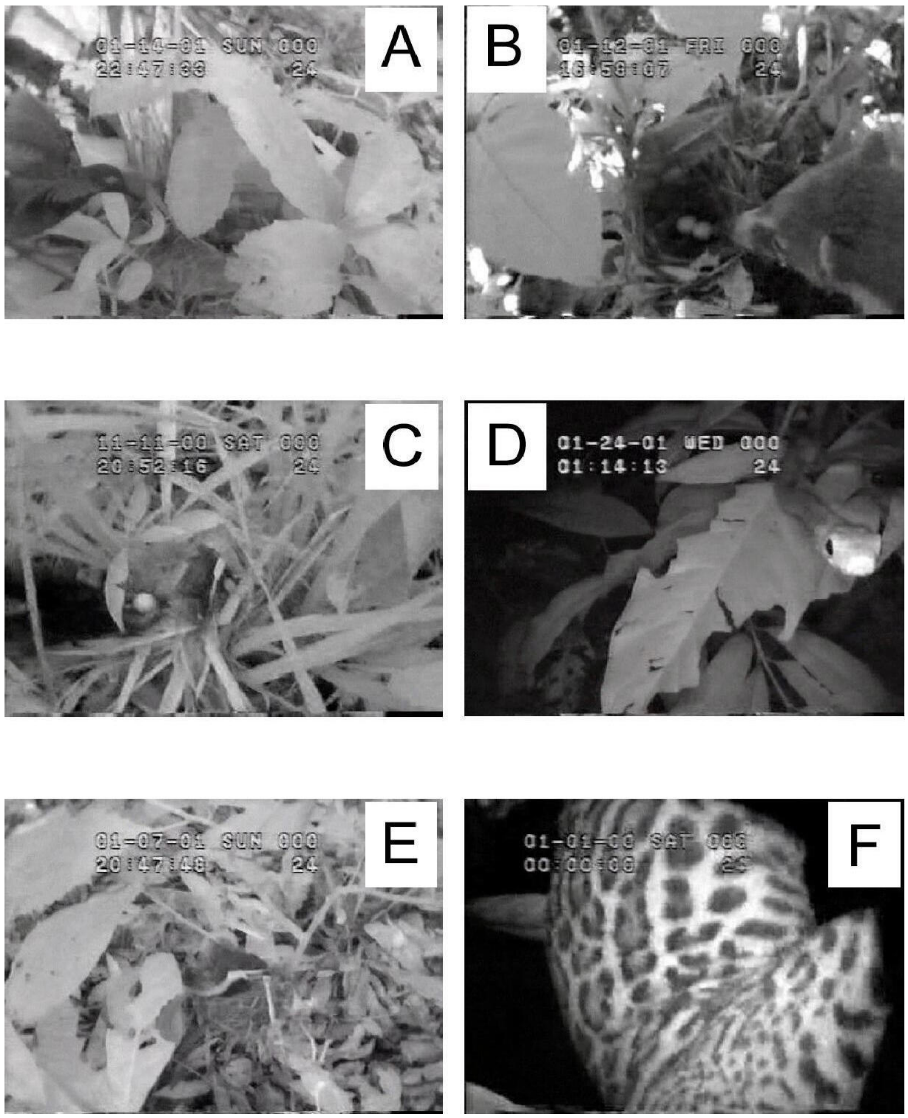

FIG. 1. Digitized images captured from videotapes: (A) male Chestnut-backed Antbird on left displaying to a snake coiled in nest and eating a nestling, (B) white-nosed coati on right about to eat the two eggs in a Chestnut-backed Antbird nest, (C) white-faced capuchin's two arms on left stealing the egg from a Chestnut-backed Antbird nest, (D) snake leaving after depredating a Spotted Antbird nest, (E) head of adult snake (center of image) eating the nestlings of a Spotted Antbird, and (F) ocelot seen sideways as it "plays" with the camera. Time stamps on images incorrectly display actual time. See Fig. 2 for times of predation events.

the eggs in the antshrike nest and we saw no evidence that they even looked into the nest.

Timing of predation events. No predation occurred at night. All visits by predators were

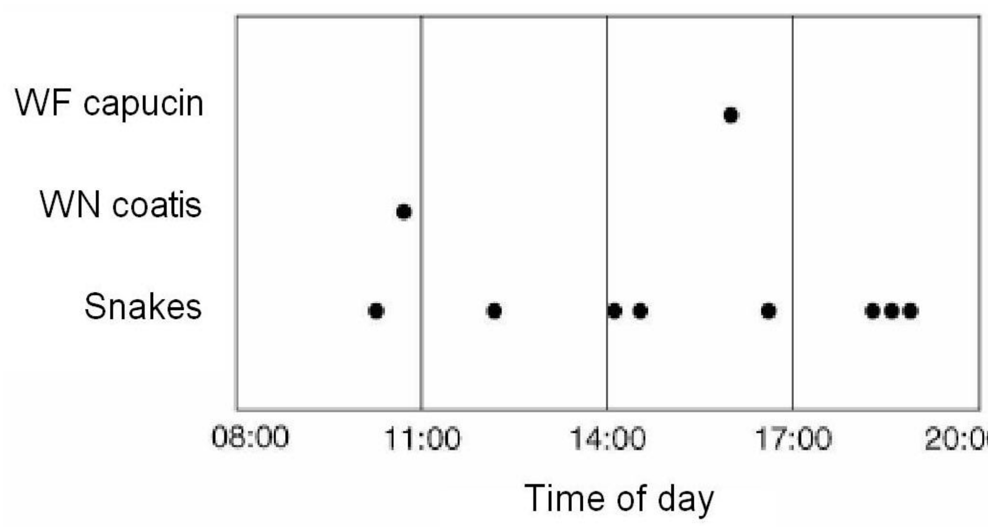

FIG. 2. Timing of visits to nests on Barro Colorado Island by three types of predators (WF Capuchin, white-faced capuchin; WN Coatis, white-nosed coatimundis; Snakes, Neotropical Bird Snake). Each circle represents one predation event. Sunset occurred between 18:30 and 19:00.

during the day, particularly late in the afternoon and near dusk (Fig. 2). Snakes tended to visit more in the late afternoon and near dusk.

Seven of ten predations occurred during incubation and three during the nestling phase. Few nests survived into the nestling phase, so those where we recorded consumption of nestlings were of nests we first found with nestlings. Detailed analysis of timing of predation indicated that nests were six times more likely to be depredated during the first week after egg-laying was completed than during any subsequent week (Rompré & Robinson in prep).

Nest condition after predation. Only one of the ten depredated nests showed any signs of disturbance. None of the nests depredated by snakes nor the nest depredated by the monkey was disturbed. The nest visited by coatis was completely destroyed.

Effect of video monitoring on behavior and predation. A Checker-throated Antwren (*Myrmotherula fulviventris*) nest was abandoned because of camera placement, so we have excluded it from analyses. For all other nests, parents took 83.5 ± 122.4 min (mean ± SD) to return to the nest. When camera placement occurred during the nestling period, parents returned more quickly (4.7 ± 4.7 min, N = 3) than if placement occurred during incubation (105 ± 125 min, N = 11, $U = 0.5$, $P = 0.01$). Otherwise, we saw no evidence that birds behaved unusually with cameras near the nests.

Cameras had little effect on risk of nest predation. The 95% confidence intervals for daily survival rates at Spotted Antbird nests were 0.939–0.983 and at Chestnut-backed Antbird nests were 0.763–0.914. Observed daily survival rates of nests with cameras fell within each range of confidence intervals (Spotted Antbird, 0.974, $P = 0.59$; Chestnut-backed Antbird, 0.837, $P = 0.22$).

Bird reactions to nest predators. Most predation events were brief, ranging from 3 s in the case of the monkey predation to 49 min when two Chestnut-backed Antbird nestlings were eaten by a small snake. From what was visible in our video images, which covered a radius around each nest of about 2 m, in only three cases were adult birds at the nest at the time of predation. An incubating female Chestnut-backed Antbird fled when coatis depredated her nest and we saw no evidence of defense at that nest. In the aforementioned snake predation which took 49 min, the pair of Chestnut-backed Antbird arrived 4 min after the snake and attacked it unsuccessfully for 45 min while the snake consumed the two nestlings (Fig. 1A). Attacks included physical contact of beaks with the snake and repeated vocalizations and wing-spreading displays. Similar behavior was recorded at another Chestnut-backed Antbird nest where both parents unsuccessfully defended the nest against a juvenile snake for nearly 4 min.

Nevertheless, not all Chestnut-backed Antbird defensive behavior and attacks on *Pseustes* were unsuccessful. In one instance, a *Pseustes* snake appeared one evening at 17:35 when no adults were present. It made its way around the nest, put its head in the nest, but did not eat the one egg. Two days later, the male Chestnut-backed Antbird was incubating and at 08:00 it quickly fled the nest then returned within a few seconds to begin attacking a snake at the nest. The male pecked the snake and it fled without eating the egg. Five days later a different snake arrived at 12:10 and ate the egg at which time no adult antbirds were seen at the nest.

DISCUSSION

Eighty percent of nest predation observed by videography was by one species of snake. The prevalence of snakes contrasts strongly with anecdotal observations collected from the nearby mainland where most predations were by birds (Robinson & Robinson 2001). Those mainland observations came primarily from forest edges. Similarly, Skutch (1960, 1971) published many anecdotal observations of predation along forest edges in Costa Rica. Most of his observations were of birds eating eggs or nestlings, but he did see a few snakes and even fewer mammals depredating nests. Whether the differences between the anecdotal observations and our camera results are attributable to habitat, observation method, or an island effect are unclear.

To the extent that we can generalize our results to other lowland Neotropical locations, the importance of snakes has implications for interpretation of results from many previous nest predation studies. Because of the difficulty of finding songbird nests in many tropical habitats, artificial nests baited with quail or finch eggs have been used many times to estimate predation. We are learning that nest predatory snakes search by using visual cues of parental activity near nests (Weatherhead & Blouin-Demers 2004). Such cues are obviously absent from artificial nests. Furthermore, snakes may use heat as a signal that eggs have been discovered because snakes routinely ignore cool quail eggs (Marini & Melo 1998). In addition, artificial nests with quail eggs may be depredated more often by mammalian predators than are real nests (Thompson & Burhans 2004, Robinson *et al.* 2005). Therefore, conclusions drawn from artificial nest studies in tropical environments should be viewed with caution (Roper 1992).

Like other camera studies from North America (Thompson *et al.* 1999, Pietz & Granfors 2000), we found that condition of nests after predation should not be used to assess predator identity. Many past studies have assumed that mammals will disturb or destroy nests. Only the nest depredated by coatis in our study was disturbed. The ground nest depredated by a monkey was undisturbed. Although our records of mammal depredations were few, they are consistent with comments cautioning against use of nest condition as a predictor of predator identity (Larivière 1999).

Nest defensive behavior was effective only once, when a Chestnut-backed Antbird chased a small snake away from its nest with eggs. Every other time, adults had no success thwarting predation attempts, despite some cases where aggressive attacks continued for more than 30 min while snakes consumed nestlings. Our observation that few nests were lost to mammals is inconsistent with the longstanding hypothesis that the cause of local extinctions of understory birds from Barro Colorado Island is reproductive failure as a result of unusually high numbers of mesopredatory mammals. The preponderance of snakes does not exclude the mesopredator release hypothesis altogether, however, because snakes can also be considered mesopredators. Instead of the widely held view that extinction of big cats allowed nest-predatory mammal populations to increase unchecked, leading to unsustainably high levels of nest predation, an alternative food web alteration involving snakes should be considered. Perhaps rarity or loss of large snake-eating raptors has allowed *Pseustes* populations to increase over that expected in mainland forests where raptors remain. Several hawk-eagles, forest-falcons, and accipiters are now extremely rare or absent from Barro Colorado Island (Robinson 1999, 2001) compared to nearby mainland forests (Robinson *et al.* 2000a), consistent with this alternative mechanism of mesopredator release. However, we know of no comparative assessments of snake abundance between mainland and island. Furthermore, no camera studies have yet been conducted on the mainland to ascertain the magnitude of nest predation by snakes. Nonetheless, our results indicate that the textbook view of why understory forest birds have disappeared from Barro Colorado Island needs further investigation.

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