



Nest Predation in a Neotropical Forest Occurs During Daytime

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APPENDIX 2. House Sparrow specimens (study skins) measured for wing length. Specimens were obtained from six introduced and geographically separate populations in North America, each sampled during two or more years throughout the 20th Century.

Museum of Vertebrate Zoology, University of California, Berkeley ($n = 344$):
12557, 12558, 12561–12566, 12568, 23342–23351, 23405, 23406, 24461–24463, 24521, 24689–24743, 24748, 24750–24755, 24760–24770, 26503–26527, 26529–26556, 26558, 26559, 95923–95927, 182585–182597, 182599, 182601–182751, 182756–182764, 182766, 182791

University of Kansas Natural History Museum & Biodiversity Research Center, Lawrence ($n = 516$):

10916, 10917, 13020, 13021, 13028, 13030, 13031, 42174, 42175, 42180–42184, 42186–42197, 42201, 42202, 42211–42219, 42222, 42226–42229, 42231–42250, 42252, 42253, 42255–42268, 42270–42284, 42301, 42418, 42420–42438, 42443, 42446, 42448–42464, 42507–42512, 42527, 42528, 42530–42535, 42537–42542, 42544–42549, 42553, 42554, 42557–42563, 42569–42573, 42576, 42578, 42583–42587, 42590, 42593–42595, 42597–42601, 42610–42612, 42614–42616, 42621, 42622, 43116, 43118, 44174–44191, 44193–44243, 44467–44509, 44534, 44535, 44720–44761, 44765–44808, 45338, 45425, 50042, 76485–76487, 76494–76525, 77717–77796

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NEST PREDATION IN A NEOTROPICAL FOREST OCCURS DURING DAYTIME

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Abstract. Alexander Skutch suggested that the threat of nest predation on tropical birds favors reduced activity near their nests. This hypothesis assumes that nest predation occurs during the day when adult birds are active, but few studies of tropical species have reported distributions of nest losses during the day-night cycle. We used thermistors placed in nests to record the time of nest predation events for species of understory rainforest birds during the incubation period. In our study, 14 of 21 nest-predation events (67%) occurred between 11:00 and 18:00 (EST), and none took place at night, between 19:00 and 06:00. Clearly, nest predation during incubation was primarily diurnal. Although a major premise of Skutch's hypothesis is supported, further research is needed to determine whether diurnal predators are attracted to nests by the movements of parent birds, begging of offspring, or other cues.

Key words: nest activity, nest attentiveness, nest predation, parental investment, Skutch hypothesis, understory rainforest birds.

La Depredación de Nidos en un Bosque Neotropical Ocurre durante el Día

Resumen. Alexander Skutch sugirió que para las aves tropicales, la amenaza de depredación del nido favorece un comportamiento de actividad reducida cerca del mismo. Esta hipótesis asume que la depredación ocurre durante el día, cuando las aves adultas están activas. Sin embargo, pocos estudios sobre especies tropicales han analizado la distribución de las pérdidas de los nidos durante el ciclo día-noche. Colocamos termistores en los nidos de especies de sotobosque para registrar el momento de los eventos de depredación durante el periodo de incubación. En nuestro estudio, 14 de 21 eventos de depredación (67%) ocurrieron entre las 11:00 y 18:00 horas (EST) y ningún evento de depredación ocurrió durante la noche, entre las 19:00 y 06:00 horas. Claramente, la depredación durante el periodo de incubación fue diurna. A pesar de que la principal premisa de la hipótesis de Skutch es apoyada por estos datos, se requiere de más investigación para determinar si los depredadores diurnos son atraídos

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al nido por los movimientos de los padres, por el comportamiento de sollicitación de los polluelos o por otras señales.

More than 50 years ago, Alexander Skutch (1949) suggested that tropical birds respond to the high risk of nest predation by reducing activity at their nests. He argued that predators cue in on begging by chicks or parental activity near nests, and that more activity leads to greater probability of nest predation. This long-standing hypothesis has been evaluated by comparing rates of predation during the incubation and nestling periods (Ricklefs 1969, Roper and Goldstein 1997, Farnsworth and Simons 1999) and subsequent to experimental manipulation of brood size (Young 1996, Styrsky et al. 2005). Results to date are not definitive, but they have confirmed neither that activity at nests increases nest predation, nor that reduced parental investment in response to predation risk is responsible for the small clutches of tropical birds (Ricklefs 1977).

Feeding rates observed in comparative and experimental studies generally support Skutch's (1985) prediction that adult birds reduce their activity and nest attendance in response to predation risk (Conway and Martin 2000, Ghalambor and Martin 2001). The impact of predation risk on parental behavior also should pertain to the incubation period, during which adult birds attending nests are exposed to predators. A prediction of the activity hypothesis, equally applicable to the incubation and nestling periods, arises from the basic premise that if Skutch's hypothesis were correct, substantial predation would occur during the day when birds are active.

Data on the timing of predation events at nests are scarce. The few studies conducted at temperate latitudes are contradictory, reporting either primarily nighttime predation (Lariviere and Messier 2001, Stake and Cimprich 2003, Carter et al. 2007) or more frequent daytime predation (King and DeGraaf 2006). Among tropical birds, we are aware only of ten daytime predation events reported for two species of antbirds on Barro Colorado Island, Panama (Robinson et al. 2005). In the present study, we document the timing of nest predation events during the egg stage for several species of passerine birds in lowland moist forest of central Panama. If predation occurred primarily during the night, when adult birds were sitting quietly on their nests, the hypothesis that predation pressure leads to the evolution of reduced nest activity and such associated traits as small brood size would be weakened. Daytime predation would be consistent with Skutch's hypothesis, although further observations would be needed to determine whether predators in the tropics are visually or acoustically oriented toward the movements of adult birds at the nest or the begging calls of chicks.

METHODS

DATA COLLECTION

We conducted the study from May through July 2003 and 2004 in Soberania National Park, which includes 22 000 ha of contiguous lowland rainforest in central Panama (9°9'35"N, 79°44'36"W). Although the forest in Soberania is secondary to mature secondary, having regenerated within the last two centuries, a full complement of predators has been observed in the area (Robinson et al. 2000).

The focal species consisted of one manakin (the Red-capped Manakin, *Pipra mentalis*), three flycatchers (the Ochre-bellied

Flycatcher, *Mionectes oleagineus*; Southern Bentbill, *Oncostoma olivaceum*; and Golden-crowned Spadebill, *Platyrinchus coronatus*), and five antbirds (the Checker-throated Antwren, *Myrmotherula fulviventris*; White-flanked Antwren, *Myrmotherula axillaris*; Spotted Antbird, *Hylophylax naevioides*; Dusky Antbird, *Cercomacra tyrannina*; and Western Slaty Antshrike, *Thamnophilus atrinucha*). The manakins and flycatchers employ a female-only incubation strategy, while the antbirds are biparental incubators. Most of the focal species build open cup-shaped nests and lay two-egg clutches. However, *Mionectes* builds a pyriform nest and lays two- to four-egg clutches, with three eggs being most common. Nest success rates during the incubation and nestling stages combined ranged from 12.3% to 39.5% for these species in Central Panama in 1996 and 1997 (Robinson et al. 2000). Most of the focal species probably re-nest several times during a typical breeding season (Roper 1996, Styrsky 2003).

All nest searching was conducted at least 1 km from forest edges, although some nests included in the study were found close to a one-track dirt road that was used infrequently. Nests of the focal species were located by following adult birds carrying nesting material and by scanning vegetation for nests while walking through the forest. When clutches were completed, we monitored incubation rhythms using iButton Thermochron temperature data-loggers (Dallas Semiconductor Corporation, Dallas, Texas) and, primarily, two-channel HOBO data-loggers (Onset Computer Corporation, Pocasset, Massachusetts). The thermistors (27-10K4A801, Onset Computer Corporation, Pocasset, Massachusetts) attached to HOBO data-loggers and the self-contained iButtons were placed at the bottoms of nest cups, as close to the eggs as possible, slightly off center. Thermistor leads were threaded through the nest material and were not visible to a bird sitting on its nest.

Nests were checked and data were downloaded every three to four days. Data-loggers were reset after downloading data as long as nests contained eggs. We judged nests to be depredated if one or more of the eggs were missing and the nest was torn, or if all of the eggs were missing and the nest was either torn or intact. Nests that had fallen due to failed support or having been hit by falling debris were not considered to have been depredated.

The accuracy and resolution of the data recorded by the iButtons and data-loggers, and the reaction of birds to the presence of the former were assessed by observing many of the nests containing iButtons for one- to two-hour periods and by videotaping nests. We found that the iButtons and thermistors registered arrivals and departures of birds almost instantaneously as abrupt changes in temperature, and that birds quickly returned to nests after data-loggers were emplaced.

We did not extend observations into the early part of the nestling period because, after a few days, nestlings were able to maintain near constant temperatures in the nests, and adult absences could thus not be detected. Instead, we transferred our temperature recorders to other nests with eggs.

DATA ANALYSIS

We estimated daily predation rates and nest success during the incubation period for the study species using the Mayfield method (Mayfield 1961, 1975, Farnsworth et al. 2000). We determined the times of arrivals and departures of adults to and from nests by abrupt temperature changes revealed on graphs of the temperatures recorded by iButtons and HOBO Loggers for each nest during each observation period (Joyce et al. 2001). A decrease

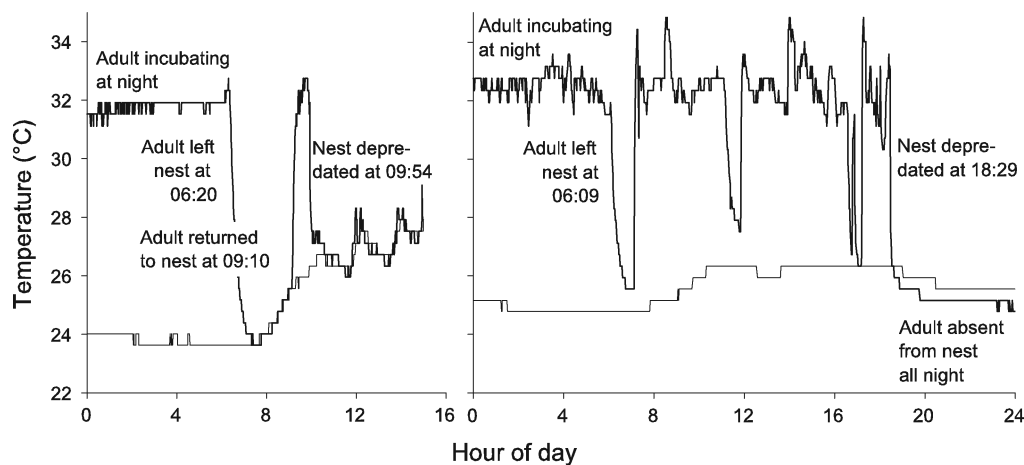


FIGURE 1. Left: Nest temperature record for one nest of the White-flanked Antwren (*Myrmotherula axillaris*) on 5 April 2004. The incubating adult left the nest shortly after dawn for an extended period of foraging. The nest was depredated 44 min after the adult returned to the nest in midmorning. Right: Nest temperature record for one nest of the Checker-throated Antwren (*Myrmotherula fulviventr*) on 19 June 2004. The nest was depredated in late afternoon, approximately 1 hr and 15 min after the adult returned from a brief spell off the nest. Both nests were in the understory of second growth forest in Soberania National Park, central Panama. Thicker lines indicate nest temperature; thinner lines indicate ambient temperature.

in temperature after a period of stable or increasing temperature signified the departure of an adult from the nest, and an increase in temperature after a period of stable or decreasing temperature signified an arrival (Fig. 1). Because birds sometimes return to their nests and attempt to incubate for a short period after nests have been depredated, we could not document the exact times of all predation events. However, we were able to distinguish diurnal (between 06:00 and 18:00 (EST) and nocturnal (between 18:00 and 06:00) events with reasonable certainty. We chose 06:00 and 18:00 as cutoff points because these times generally mark the first departures in the morning and the last arrivals in the evening, respectively. During the study period, the interval between sunrise and sunset varied between 12 hr 14 min and 12 hr 43 min, and civil twilight extended the visible period by about 20 min at the beginning and end of the day (List 1966). Depredation events during the interval between nest checks were evident from the disappearance of eggs, and their timing could be estimated by prolonged departures of incubating adults breaking the normal pattern of daytime

on and off bouts or constant nocturnal incubation (Fig. 1), followed by an absence of further incubation. Statistical tests of contingency tables (χ^2 and G statistics) were performed in Excel (Microsoft Corporation, Redmond, Washington) spreadsheets using the Poptools Version 2.7.5 add-in software (Hood 2006). Circular statistics to test for periodicity of events through the day-night cycle are based on the Rayleigh test (Fisher 1993).

RESULTS

We monitored 90 nests containing one or more eggs. We placed data-loggers in 43 nests, 21 of which were depredated during the incubation stage. Average daily nest mortality rates for the study species ranged from 0.9% for *P. coronata* to 9.1% for *O. olivaceum* (Table 1). Estimated nesting success (during the incubation period only) ranged from 17% for *O. olivaceum* to 83% for *P. coronata* (Table 1).

TABLE 1. Nesting success of nine species of understory rainforest birds in central Panama during April–July 2003 and 2004. Daily mortality rate (DMR) is the number of predation events divided by the total number of days eggs were present in nests (i.e., exposure days; Mayfield 1975). The Mayfield nesting success is calculated from the exponential rate of decrease per day in the proportion of surviving nests and the length of the incubation period, including laying (Robinson et al. 2000). N is the number of nests of each species.

Species	N	Incubation period (days)	Exposure days	DMR (% day ⁻¹)	Mayfield (%)
<i>Thamnophilus atrinucha</i> (Western Slaty Antshrike)	21	16.1	195	5.1	43
<i>Myrmotherula fulviventr</i> (Checker-throated Antwren)	18	19.6	218	3.6	48
<i>Myrmotherula axillaris</i> (White-flanked Antwren)	5	17.5	54	1.9	71
<i>Cercomacra tyrannina</i> (Dusky Antbird)	7	18.9	65	1.5	75
<i>Hylophylax naevioides</i> (Spotted Antbird)	7	17.9	80	3.8	51
<i>Oncostoma olivaceum</i> (Southern Bentbill)	4	19.4	44	9.1	17
<i>Mionectes oleagineus</i> (Ochre-bellied Flycatcher)	8	23.3	100	3.0	50
<i>Platyrinchus coronatus</i> (Golden-crowned Spadebill)	7	20.2	110	0.9	83
<i>Pipra mentalis</i> (Red-capped Manakin)	13	20.8	115	4.3	40

TABLE 2. Timing of predation events in 21 nests of small forest passerine birds during the incubation period in central Panama.

Species	Year	Month	Day	Time
<i>Pipra mentalis</i>	2004	June	18	0812
<i>Hylophylax naevioides</i>	2004	July	5	0851
<i>Myrmotherula fulviventr</i>	2004	Apr	19	0916
<i>Oncostoma olivaceum</i>	2004	Apr	28	0937
<i>Myrmotherula axillaris</i>	2004	Apr	5	0954
<i>Oncostoma olivaceum</i>	2004	Apr	26	1136
<i>Myrmotherula fulviventr</i>	2003	July	8	1300
<i>Pipra mentalis</i>	2004	May	17	1325
<i>Platyrinchus coronatus</i>	2004	July	3	1330
<i>Mionectes oleagineus</i>	2004	June	23	1436
<i>Myrmotherula fulviventr</i>	2004	July	5	1450
<i>Oncostoma olivaceum</i>	2004	Apr	9	1459
<i>Thamnophilus atrinucha</i>	2003	July	17	1507
<i>Thamnophilus atrinucha</i>	2003	July	1	1538
<i>Hylophylax naevioides</i>	2004	May	23	1539
<i>Oncostoma olivaceum</i>	2004	Apr	6	1552
<i>Myrmotherula fulviventr</i>	2004	Apr	28	1618
<i>Hylophylax naevioides</i>	2004	May	9	1642
<i>Myrmotherula fulviventr</i>	2004	Apr	20	1711
<i>Myrmotherula fulviventr</i>	2004	June	19	1829
<i>Cercomacra tyrannina</i>	2004	July	6	1900

With regard to nests with data-loggers, 14 of 21 nest-predation events (67%) occurred between 11:00 and 18:00, and none took place between 19:00 and 08:00 (Table 2). When predation events were binned into 4-hr periods centered on 00:00, 04:00, 08:00, . . . , the distribution was significantly heterogeneous ($\chi^2_5 = 20.4$, $P = 0.001$). The average time of day at which predation occurred was 13.9 hr \pm 3.2 SD (i.e., about 14:00). Using circular statistics, the average time of predation events was 13.6 hr, and the Rayleigh test was highly significant ($Z = 6.6$, $P = 0.001$), confirming that predation events were significantly clumped during daylight hours.

DISCUSSION

We found that, in this sample of tropical understory birds, predation on nests with eggs occurred exclusively during daylight hours and at dusk. We emphasize that our study was conducted only during the egg stage of the nesting cycle; different predators having different activity patterns might be responsible for losses during the nestling period. Nonetheless, our results imply that because nest predators are diurnal, they potentially could make use of the activity of parents and vocalizations of young to locate nests, providing support for the parental investment models of Skutch (1985) and Martin (2002). Ghalambor and Martin (2001) showed in an experimental study that adult birds reduce nest attendance where the perceived risk of nest predation is high. However, direct comparisons of the frequency and intensity of begging vocalizations on rate of nest predation have produced varying results (Leech and Leonard 1997, Halupka 1998). Moreover, experimental manipulation of brood size and activity levels in two tropical species failed to establish a relationship between activity and probability of predation (Young 1996, Styrsky et al. 2005). Thus, although predators undoubtedly influence the evolution of parental behavior at the nest, including

nest structure and placement (Fontaine et al. 2007), it is as yet unclear whether predation pressure selects for reduced nest attendance and reduced brood size in tropical birds.

Predators on the nests of small songbirds in the moist forest understory of lowland central Panama appear to be primarily diurnal. Robinson et al. (2005) recorded 10 predation events on nests of the Spotted Antbird and Chestnut-backed Antbird (*Myrmeciza exsul*) during the incubation period on Barro Colorado Island, central Panama. All the events occurred during daylight hours, and the colubrid snake *Pseustes poecilinotus* was identified as the predator in eight cases. Other important nest predators, such as the Keel-billed Toucan (*Ramphastos sulfuratus*; C. Tarwater, University of Illinois Champaign-Urbana, pers. comm.) also are diurnal.

Further study is needed in diverse tropical environments to identify nest predators and to determine how they locate nests. Video records of activity at nests at all stages of the nest cycle, additional experiments manipulating brood size or behavioral cues, and comparisons of parental activity under different local densities of predators, perhaps contrasting island and mainland environments, would be especially informative for further evaluation of Skutch's hypothesis.

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HISTORIC GENETIC STRUCTURING AND PARAPHYLY WITHIN THE GREAT-TAILED GRACKLE

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Abstract. The Great-tailed Grackle (*Quiscalus mexicanus*) and Boat-tailed Grackle (*Q. major*) are sister species that have expanded their ranges during historical times. This expansion has created an area of sympatry between these species in Texas and Louisiana, and between distinctive Great-tailed Grackle subspecies in the southwestern United States and northern Mexico. We investigated the evolutionary histories of both

species using mitochondrial DNA sequence data and modern phylogenetic methods. Our results reveal genetic structure within Great-tailed, but not Boat-tailed Grackles. Great-tailed Grackles are separated into two clades, but range expansion in the north has led to secondary contact between them. Boat-tailed Grackles are monophyletic and are embedded within the Great-tailed Grackle assemblage, rendering the latter paraphyletic. These results reveal a complex phylogeographic pattern caused by recent range expansion and secondary contact of once allopatric units.

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Key words: grackle, mitochondrial DNA, paraphyly, phylogeog-
raphy, *Quiscalus*, range expansion.

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