

eye movement (REM) sleep each night is shorter (Zepelin and Rechtschaffen 1974, Zametkin et al. 1979). We attempted to relate REM sleep to spontaneous blinking in the species we studied, but with little success because so little is known about the REM sleep of birds. Nonetheless, three reports suggest that owls (Berger and Walker 1972) have episodes of REM sleep that are shorter (5% of total sleep time) than those of Rock Doves (Walker and Berger 1972) and two falconiforms (Rojas-Ramirez and Tauber 1970), all of which are diurnal and have periods of REM sleep averaging 7–10% of their total sleep time. This relationship between diurnal and nocturnal forms is opposite to that reported for mammals. The limited data available and the primitive nature of REM sleep in birds (Berger and Walker 1972) may, however, preclude a significant correlation.

Phasic regulation of neuroendocrine, metabolic, reproductive and motor activity by light is well known in birds. For example, in the Mallard exposure of retinal receptors responsive only to red or orange light stimulated gonadal growth (Benoit 1964). Similarly, under natural conditions, the foraging and reproductive activities of many avian species are closely related to daily and seasonal changes in photoperiod. While these long-term effects of light have been defined, the function of the brief pulses of light produced by spontaneous blinking has not.

The primary function of spontaneous blinking is generally considered to be the cleansing and irrigation of the eyes. Ponder and Kennedy (1928), however, noting that its rate was remarkably constant and independent of such factors as light, temperature, humidity, and the integrity of cranial nerves II through VI, concluded that blinking is centrally mediated and that it serves functions beyond simple cleansing. Blinking causes regular brief exposure of the retina to external light through the red/orange filter of the closed lids or nictitating membrane (Crawford and Marc 1976). Eyeblinks have been shown to evoke electrical potentials and multiple neuronal activity in the visual cortex and subcortical nuclei of cats (Stevens and Livermore 1978). Such periodic interruption of the light striking the retina may provide the avian central nervous system with a constant source of pulsed stimulation with which to couple such cyclic events as the release of biogenic amines, endocrine function, or motor activity. While differences in blinking rate between nocturnal and diurnal species

have been shown in this study, their functional significance must await further investigation.

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NEST PREDATION IN INSULAR AND MAINLAND LOWLAND RAINFOREST IN PANAMA

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Reproductive success in birds is commonly measured through analysis of nesting mortality (Snow and Snow 1963, Skutch 1966, Lack 1968, Oniki 1975, Kuleza 1980). Predation is a primary cause of nesting mortality and thus exerts a strong influence on reproductive behavior (Cody 1971). Nest predation also may be a major cause of extirpation for island birds (Greenway 1958).

Many species of birds have vanished on Barro Colorado Island (BCI), Panama, since the island was formed in 1914 (see Willis and Eisenmann 1979, Karr 1982 for current

extirpation lists) and Willis (1974) suggested that predation may be a factor in the loss of some of these species. Willis and Eisenmann (1979) reported that small mammal and snake populations, "especially the nest robbing *Pseustes poecilonotus* and *Spilotes pullatus*," have flourished on the island since its establishment as a reserve. Karr (1982) suggested that the increased number of small predators on BCI, compared with adjacent mainland, is the result of lack of hunting on the island, and to a lesser extent, the lack of large predators. Higher densities of small predators have been predicted to coincide with greater loss of nests and nestlings (Oniki 1979).

In an effort to test the hypothesis that predation rates are higher on BCI than on similar mainland habitat, we placed artificial nests in forests on BCI and on adjacent Panama mainland. This experimental procedure also allowed us to examine effects of nest location and nest type on predation rates.

METHODS

We placed nests in two rainforest sites during March 1981. The mainland site was adjacent to Limbo Hunt Club (LHC),

TABLE 1. Number of artificial nests preyed upon at LHC and BCI. *n* represents the sample size; "Pred" is the number of nests lost to predators. Percentage of nests lost to predation is in parentheses.

Height of nest	LHC						BCI					
	Open cup		Closed		Total		Open cup		Closed		Total	
	<i>n</i>	Pred	<i>n</i>	Pred	<i>n</i>	Pred	<i>n</i>	Pred	<i>n</i>	Pred	<i>n</i>	Pred
Ground	17	1 (6)	17	1 (6)	34	2 (6)	9	9 (100)	8	6 (75)	17	15 (88)
1 m	17	2 (12)	17	0 (0)	34	2 (6)	9	2 (22)	9	0 (0)	18	2 (11)
2 m	16	0 (0)	17	0 (0)	33	0 (0)	7	1 (14)	9	0 (0)	16	1 (6)
Total	50	3 (6)	51	1 (2)	101	4 (4)	25	12 (48)	26	6 (23)	51	18 (35)

approximately 8 km north of Gamboa, on the Pipeline Road area of Parque Nacional Soberania. The second site was on BCI on Wheeler Trail, near the Barbor-Lathrop junction. The BCI site was selected to closely approximate the forest structure at LHC. Both sites represent mature lowland forest. A more complete description of the areas may be found in Croat (1978) or Willis and Eisenmann (1979) for BCI, and Karr (1971) for LHC.

Artificial wicker nests (purchased from a distributor of pet supplies) were lined with fresh leaves and placed in the forest 5–10 m from a foot trail at 10–15 m intervals. Two types of nests, open cup (diameter at widest point 10 cm, height at deepest point 6 cm) and closed (opening 2.5×4 cm, width 7.5 cm, height 9 cm), were placed at ground level and at approximately 1 and 2 m. Precise height varied slightly due to variation in availability of suitable nest sites (e.g., fork in a tree). Because our goal was to obtain information on relative predation pressure on insular and mainland areas, rather than absolute rates of predation, we made no attempt to approximate the appearance of real nests other than to line nests with fresh vegetation. We assumed that predators at LHC and BCI forage in a similar manner and therefore felt that comparison of nest predation between the two areas would be valid.

One or two quail eggs (probably *Coturnix coturnix*, average size 28×23 mm) purchased from a local supermarket, were placed in each nest. Artificial clutch size was varied so as to examine the effect of clutch size on the probability of nest predation. Clutches above two were not used due to limited availability of quail eggs and because many tropical undergrowth birds have small clutches (i.e., two eggs or fewer, see Skutch 1976). Due to lack of time, nests were left in the forests for only two days. Nests were put in place during late afternoon and checked 24 and 48 h later. Fifty-one nests were put out at BCI, and two trials of 51 and 50 nests were conducted at LHC; we did not have enough time at BCI to run two trials. Predation was assumed if eggs or nest were missing. The Fischer Exact Probability test corrected for differences in sampling intensity (number of nests), was used to test for differences in the number of nests preyed upon.

RESULTS AND DISCUSSION

We found no difference in predation pressure between nests containing one or two eggs so data were lumped. Also, data at LHC were combined since replicated trials had similar predation pressure (<6% difference).

Open cup nests were not preyed upon significantly more than were closed nests ($P > 0.05$), although the insular site just misses significance ($P = 0.06$; Table 1). At both sites, however, predation was greater on open nests and lack of significance may reflect inadequate sample size or duration of experiment. Lack (1968) and Oniki (1975) suggested that open nests are more susceptible to predation and our results support this idea.

Closed nests may be difficult to break open, thus accounting for lower predation rates (Oniki 1979). We once found a closed nest at LHC about one meter from its original location; although the eggs were intact, the nest

was deformed. No environmental factor (wind, fallen branch) appeared responsible and we suspect that the nest was handled by a mammal, possibly a coatimundi (*Nasua narica*). In addition, a closed nest at ground level disappeared entirely; we suspect that a mammal removed the nest while trying to extract the eggs.

Nests located on the ground at BCI, including both open and closed, suffered more predation ($P < 0.001$) than those above ground (Table 1). Frequency of predation on ground nests also was higher on the mainland site, but not significantly so.

Predation pressure on open and closed ground nests was much greater on BCI ($P < 0.001$) than on the mainland. Predation pressure on nests above ground level was not statistically different between the two study sites. However, frequency of nests preyed upon was higher for open cup nests above ground level at BCI (Table 1). No closed nests above ground were preyed upon at either site. What is most remarkable about these findings is the magnitude of these differences. All open cup nests on the ground were lost to predators at BCI compared to only 6% at LHC. Closed ground nests at BCI experienced 75% predation; only 6% were preyed upon at LHC.

A confounding factor in our results is the possibility that small predators might be more attracted to human objects as possible food sources at BCI. If this is the case, then incidence of predation on the island may be greatly overexaggerated. However, in light of the higher densities of small predators on BCI and the absence of any differences in predation pressure above ground, we feel that this factor does not seriously affect our results.

We cannot say how the results might have changed if nests had been left out for 14 to 18 days to approximate a normal incubation period. Janzen (1978) in a similar study in Costa Rican habitats, put quail (one or five eggs/clutch) and chicken eggs (one egg/clutch) directly on the ground and left them out for 18 days. Frequency of predation, on one-egg clutches, during the first 48 h of the study was similar to that obtained at LHC; no chicken eggs were taken during this period and only one of eight (12.5%) quail eggs was removed. This compares with 1 of 17 (6%) taken from open cup nests at LHC. Eventually, 50% and 62.5% of quail and chicken eggs, respectively, were taken after 18 days. If artificial nests at LHC followed a similar pattern, number of nests plundered would not approach those taken at BCI in just 48 h.

Predation pressure on experimental nests may overestimate real predation rates. Handling of nests and eggs may leave persistent odors that attract nest predators and absence of parental defense may make experimental nests more susceptible to predation.

Kuleza (1980) compared predation on artificial and real nests in temperate woodlands and found that artificial nests overestimated mortality by as much as 15–20%. Gottfried and Thompson (1978), however, found that experimental and real nests in old fields suffered similar predation rates. Data from three species of birds nesting on or near the ground at BCI suggest that our results are realistic estimates of nesting mortality. At hatching, 82,

81, and 77% of nests were lost to predation and other causes for Ocellated Antbird (*Phaenostictus mcleannani*), Spotted Antbird (*Hylophylax naevioides*), and Bicolored Antbird (*Gymnophaps leucaspis*), respectively (Willis 1974). Even if experimental figures are off by 10% or more, predation must nonetheless exercise a strong influence on populations of species nesting on or near the ground (i.e., < 0.5 m; some antbirds, tinamous). Morton (in Karr 1982) attributed the decline in reintroduced Musician Wren (*Cyphorhinus aradus*) populations on BCI to predators on and near the ground.

Loss of bird species on BCI since formation of Gatun Lake in 1914 has been attributed to a variety of causes— island size, loss of second growth habitat, maturation of young forest, competition, lack of wet refugias, and inability to colonize (Willis and Eisenmann 1979, Karr 1982). Predation also may be a factor (Willis 1974, Karr 1982), and results from our study support this contention, especially for ground-nesting species. Nest type, however, does not seem to be as important a factor as nest location in determining predation pressure, despite a trend for closed nests to be better protected from predation. Lack of a nest-type effect may reflect the identity of nest predators. Manipulation of nests may be accomplished more readily if nest predators were mammals, and differences in predation rates of open and closed nests may only reflect differences in the rate at which nest types are found. Nests above ground, however, are probably encountered less frequently by mammalian predators (Ricklefs 1969), suggesting that, above ground, nest type may play a larger role in determining predation pressure. In our study, all occurrences of predation above ground were recorded from open cup nests. We suggest that predation by snakes may play a more important role for nests located above ground.

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ADDITIONS TO THE AVIFAUNA OF BOLIVIA, PART 2

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We here report additions to the bird species known from Bolivia that have come to light since Remsen and Ridgely (1980). Most of the specimens were collected by Richard S. Crossin on an expedition to Dptos. Santa Cruz, Chuquisaca, and Tarija, 1972–1973, for the Field Museum of Natural History (FMNH); by Roy Steinbach in Chiquitos province, Dpto. Santa Cruz, 1973, also for FMNH; or by Kenneth E. Stager and S. C. Bromley on an expedition to

Dptos. Tarija and Chuquisaca, 1957, for the Los Angeles County Museum (LACM). In the second section of the paper, we report new information concerning additional species only recently added to the birds known from Bolivia.

The following species are here recorded for the first time from Bolivia:

Aegolius harrisi. Buff-fronted Owl. Crossin collected an adult male (FMNH 293621) in cloud forest 28 km W of Comarapa, 8,400 ft. (2,560 m), Dpto. Santa Cruz, on 27 March 1973. Meyer de Schauensee (1966) recorded no Andean specimens between Ecuador and Jujuy, Argentina. There is also a recent, unpublished record from Peru: P. Hocking and G. Lopez collected two specimens (FMNH 285086, 287773) at Yurinaqui Alto, Dpto. Junín on 6 January and 6 July 1969. Further collecting may show that *Aegolius harrisi* is locally distributed in the subtropical and temperate zones of the Andes from Venezuela to northwestern Argentina. The Argentine population was