

SPONTANEOUS BLINK RATES
OF BIRDS

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The blinking activity of birds has received little attention in the scientific literature, although the subject has been studied in more depth in mammals (Wood and Saunders 1962, Zametkin et al. 1979). Mammals have characteristic species-specific blink rates that are independent of light, heat, or humidity (Blount 1927, Ponder and Kennedy 1928). They range in frequency from 0-4/min in the rat, mouse, hamster, and fox, to 8-22/min in primates, to 30-36/min in the domestic pig (Hall 1945, Stevens and Livermore 1978). Moreover, the blink rate of diurnally active mammals is more than 10 times higher than that of nocturnally active species. In this study, we measured the spontaneous blink rates of 25 species of birds and examined them for similar diurnal/nocturnal patterns. Accurate data on blink rate could provide a way of assessing the physiological condition of individual birds. Alternatively, if such rates increase with age as they do in humans (Zametkin et al. 1979), blinking may provide an estimate of age, much as external morphological features are used in certain species.

We determined the spontaneous blink rates of 25 species of birds in zoos and bird sanctuaries (Table 1). Our measurements were made between 09:00 and 15:00 generally

in daylight, but in fluorescent dim blue light in the case of the Screech Owl. Observations were made either at close range or with a spotting scope. After the bird had habituated to us (1-5 min), we counted the number of times that it blinked in 10 separate 1-min periods while it sat quietly. For most species, we used at least two individuals to determine a mean blink rate. Both bilateral and unilateral blinks as well as closure of the nictitating membrane were counted, but are not distinguished in this report.

The blink rates of most individuals and species were relatively constant under quiet, unchanging test conditions. Mean values ranged from 1.5/min for the Screech Owl to more than 50/min for the Rock Dove and Ruby-throated Hummingbird. In several species, including the White-winged Dove, Wild Turkey, and Rock Dove, blinking appeared to be correlated with head movement, suggesting that the vestibular apparatus modulates the blink reflex in these birds, as has been reported in humans (Ponder and Kennedy 1928).

Although we did not control the amount of light to which the birds were exposed, the blink rates differed little between individuals in bright light and those in the shade. Indeed, a blind Screech Owl blinked at a mean rate (1.2 blinks/min) that did not differ significantly from that of conspecifics with normal vision (1.5 blinks/min). This observation suggests that in birds, as in humans, the blink rate for individual species does not depend upon photostimulation of the retina, provided the light to which subjects are exposed is not extremely bright.

Our results also suggest that diurnally active birds blink more frequently than nocturnally active species (Table 1). In general, all species of owls blinked less than 10 times per minute, whereas diurnal species had higher mean rates. The Snowy Owl, which is active in daytime, had the highest rate among the owls.

Diurnal mammals also have considerably higher blink rates than nocturnal mammals; furthermore, their rapid

TABLE 1. Spontaneous blink rate of birds.

	<i>n</i>	Average* blink rate	Range of blink rates
Nocturnal species			
Black-crowned Night-Heron (<i>Nycticorax nycticorax</i>)	2	3.2 ± 0.8	2-4
Eastern Screech-Owl (<i>Otus asio</i>)	2	1.5 ± 0.7	0-3
Great Horned Owl (<i>Bubo virginianus</i>)	7	3.7 ± 2.5	0-7
Snowy Owl (<i>Nyctea scandiaca</i>)	3	9.0 ± 2.7	6-12
Burrowing Owl (<i>Athene cunicularia</i>)	2	2.9 ± 1.2	0-5
Barred Owl (<i>Strix varia</i>)	4	5.9 ± 3.5	2-11
Northern Saw-whet Owl (<i>Aegolius acadicus</i>)	3	4.0 ± 1.1	2-5
Diurnal species			
Scarlet Ibis (<i>Eudocimus ruber</i>)	3	41.3 ± 5.3	33-50
Roseate Spoonbill (<i>Ajaia ajaja</i>)	5	32.5 ± 4.5	24-44
Mallard (<i>Anas platyrhynchos</i>)	2	28.3 ± 3.1	22-32
Barrow's Goldeneye (<i>Bucephala islandica</i>)	2	40.1 ± 6.7	32-51
Northern Goshawk (<i>Accipiter gentilis</i>)	1	12.7 ± 1.6	10-15
Red-shouldered Hawk (<i>Buteo lineatus</i>)	1	11.8 ± 1.6	9-14
Swainson's Hawk (<i>Buteo swainsoni</i>)	3	16.8 ± 2.4	12-19
Harris' Hawk (<i>Parabuteo unicinctus</i>)	1	13.2 ± 1.6	10-16
Golden Eagle (<i>Aquila chrysaetos</i>)	4	16.8 ± 3.5	11-22
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	1	21.6 ± 5.1	13-27
Crested Caracara (<i>Polyborus plancus</i>)	1	13.5 ± 2.6	11-19
Wild Turkey (<i>Meleagris gallopavo</i>)	3	43.3 ± 7.9	31-51
Common Snipe (<i>Gallinago gallinago</i>)	1	46.9 ± 4.4	40-54
Laughing Gull (<i>Larus atricilla</i>)	4	41.0 ± 3.7	36-48
Black Skimmer (<i>Rynchops niger</i>)	1	18.8 ± 2.9	14-23
Rock Dove (<i>Columba livia</i>)	5	52.0 ± 22.1	23-88
White-winged Dove (<i>Zenaida asiatica</i>)	4	28.0 ± 5.8	19-36
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	1	53.4 ± 4.6	48-60

* Values in the table are average rates per minute ± SD. The latter refers to the variance among measurements on individual birds when *n* is 1-2.

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),