Sleep Behavior of Frogs

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Pieron (1913) established postural and threshold criteria of sleep as major elements in his definition of that behavioral state. A review of the literature and his own naturalistic laboratory observations led him to conclude that mammals, birds, and reptiles all sleep; that insects, fish and amphibians clearly fulfill the postural, but not so clearly the threshold, criterion of sleep; and that the behavior of other invertebrates defies analysis by means of his definition. Recent physiological work has added an electrographic criterion of sleep, the application of which strengthens Pieron's views on the presence of sleep in mammals, birds, and reptiles and also indicates considerable differentiation of phases of sleep within these classes of animals.

A recent study (Hobson, 1966) has shown that the bullfrog, *Rana catesbeiana*, does not fulfill either the threshold or the electrographic criterion of sleep. In brief summary, though impressively immobile and clearly at rest for long periods of time, the bullfrog remains alert, reacting with equal speed and intensity to experimental stimuli delivered at any phase of the rest-activity cycle. During periods of rest, furthermore, the brain waves of the bullfrog are of low voltage and fast electrical activity which is associated with alertness in other animals. To obtain complementary field data for this species of frog and to examine two species of tree frogs whose field behavior has been extensively studied and described (Goin and Goin, 1957; Goin, 1958) we made observations of frogs in the region of Gainesville, Florida, during the month of March, 1966.

Rana catesbeiana, normally active at night, proved impossible to observe at rest by day. In a trip around a small pond where these frogs are known to abound we saw only 6 specimens, all moving. Despite our caution, a frog would be seen only after it had begun a long leap from the edge of the pool into deeper water about 15 or 20 feet ahead of us. The extreme sensitivity of this animal to stimulation is as remarkable in the field as it is in the laboratory and it is confirmed that, in all observed cases at least, the state of rest is characterized by alertness and not by the loss of reactivity required by our definition of sleep. We cannot rule out the possibility, of course, that the bullfrog sleeps unobserved but can state that the observable behavior of this species is the same in the field as it is in the laboratory. We therefore conclude that *Rana catesbeiana* does not sleep.

Hyla squirella and *Hyla cinerea*, also nocturnally active, were invariably found to be resting by day. In a mesic hammock area we observed at least 20 specimens of each species of frog, all of which were immobile, with eyes closed, and with heads pointing toward the tips of the palmetto leaves where they rested about 2 feet above the ground. Only after moderately intense and direct stimulation such as shaking the plant, did the animals assume a crouching posture, open the eyes, and sometimes attempt to flee by leaping to a neighboring plant. In every case this sort of crude clinical testing indicated that the resting tree frogs had a clearly elevated threshold to sensory stimulation and could thus be said to be alseep by behavioral definition.

We speculate that the presence of clearcut sleep behavior in *Hyla* and its absence in *Rana* may reflect an evolutionary modification of behavior: with the adaptation of *Hyla* to a more terrestrial and arboreal mode of life, there must have developed increasing neuromuscular sophistication, as well as important changes in respiratory functions. Kleitman's evolutionary theory of sleep asserts that sleep behavior is not a primitive state but one which has evolved in parallel with increasing complexity of waking behavior. We would, therefore, expect to find correlative neurophysiological differences between *Rana* and *Hyla*. It will be of interest now to study the electrographic correlates of the putative state of sleep in tree frogs.

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