

Animal Sleep: A Review of Sleep Duration Across Phylogeny

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CAMPBELL, S. S. AND I. TOBLER. *Animal sleep: A review of sleep duration across phylogeny*. NEUROSCI BIOBEHAV REV 8(3)269-300, 1984.—Sleep duration and placement within the twenty-four hour day have been primary indices utilized in the examination of sleep function. It is of value, therefore, to evaluate these variables in a wide range of animal species. The present paper examines the literature concerning sleep duration in over 150 animal species, including invertebrates, fish, amphibians, reptiles, birds, and 14 orders of mammals. We first present annotations of almost 200 studies, including number of animals used, photoperiod employed, sleep duration per twenty-four hours and placement of sleep period within the nycthemeron. Both behavioral and electrographic studies are reviewed, as are laboratory and field studies. These data are subsequently presented in a table with representative literature citations for each species. Following the table, a brief discussion is presented concerning some methodological issues which may affect the measurement of sleep duration and some suggestions are made for future examination of sleep duration.

Sleep Sleep duration Sleep placement Behavior EEG Animals Phylogeny

IT can be argued that the two most important variables in the study of sleep are sleep duration and its placement within the 24-hr day. Traditionally, these two variables have been the primary basis for the generation of theories regarding the functions of sleep. On the one hand, Zepelin and Rechtschaffen [224] have comprehensively examined the possible relationships between sleep length and life expectancy, as well as between sleep stages and variables such as metabolic rate, brain weight and body size. On the other hand, the relationship between sleep duration and placement and environmental factors such as sleep habitat and predatory danger has been examined [5, 7, 119, 217, 218].

The present paper is not concerned with investigating such relationships or with assigning function to sleep. Our purposes were twofold. First, we wished to present, in an easily accessible format, a compilation of the existing data base concerning the duration and placement of sleep within the light-dark cycle. Secondly, we wished to examine problems which may arise in the evaluation of sleep duration in animals. These problems are principally concerned with methodological difficulties, not least of which is the definition of sleep itself.

To these ends we have carefully read and critically examined over 200 studies concerned with the sleep or rest duration of over 150 species. On one hand, it would have been possible to write this review using very strict methodological criteria as a basis for the inclusion of studies. However, we felt that the value to the understanding of the evolution of sleep provided by these studies outweighed such inadequacies as small sample size, unspecified experimental

conditions and sometimes vague criteria for the definition of sleep. Therefore, we have chosen to include any study which contained a report of sleep duration per 24 hr.

The first section presents detailed annotations of these studies. Both behavioral measures and electrographic evidence are reviewed. Likewise, both laboratory studies and field investigations, when available, are considered. While there are a number of studies concerned with the developmental aspects of the sleep process in several species, the present survey is primarily restricted to the description of sleep length of normal mature animals. In several mammalian species, especially laboratory mammals, representative studies were selected for inclusion. This decision was based on the fact that certain species have been extensively examined and there is general agreement across studies regarding sleep measures. Following this section is a comprehensive table containing measures of sleep duration and placement based on the literature reviewed.

In the final section we outline some of the more important methodological issues which may affect the measurement of sleep duration, and the reliability and validity of those values. In addition, we suggest some approaches which may aid in the future examination of sleep length across phylogeny.

THE DATA

In mammals, sleep can be reliably defined in terms of behavioral criteria. These criteria consist of: (1) the assumption of a stereotypic or species-specific posture, (2) the maintenance of behavioral quiescence, (3) an elevation of arousal

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threshold which may be reflected in the intensity of an arousing stimulus and/or the frequency, latency or duration of an arousal response, and (4) state reversibility with stimulation [52,60]. The basis for such a behavioral definition of sleep was provided by Piéron as early as 1913 [136].

By recording brain electrical activity in conjunction with behavioral observations of sleep and waking in laboratory mammals, it later became possible to develop electrophysiological criteria which have also come to be considered as reliable indicators of sleep and wakefulness. Indeed, the field of sleep research is presently dominated by the use of electrographic measurement to define sleep, often at the exclusion of behavioral observation. In effect, many sleep researchers have come to disregard the very relationship between behavior and electrophysiology upon which the worth of electrographic criteria as indicators of sleep was initially based.

Because of the close relationship between EEG and behavior in virtually all mammals and birds thus far studied, the use of electrographic measures of sleep, at the exclusion of behavioral observation, is not generally viewed as a critical methodological problem. Yet, a growing body of evidence indicates that behaviors and their usual electrophysiological correlates may become dissociated. For example, Borbély *et al.* (unpublished data) have shown that, following sleep deprivation, delta activity typically associated with behavioral sleep may appear in the EEGs of behaviorally active rats. In addition, several investigators have noted the presence of slow wave activity in non sleep-deprived, behaviorally active, rats and cats (for a review, see [201]). A recent study of sleep in three-toed sloths [47] found similar dissociations between behavioral and electrographic indices of sleep and wakefulness. Slow wave activity has been observed during behavioral waking in several species of birds, as well (for a review, see [68]).

Reptiles exhibit the same set of behaviors typical for sleep in homeotherms. As in mammals, such behavioral changes are usually accompanied by electrographic changes in brain activity. Few investigators, however, have found the EEGs of sleeping reptiles to conform to the criteria employed to define electrographic sleep in homeotherms. Hartse and Rechtschaffen [70] have argued convincingly that the high-voltage fast spiking activity which characterizes the brain activity of most reptiles during behavioral sleep is analogous to similar potentials recorded from limbic structures in mammals (VH spikes) during slow wave sleep. Consequently, these authors conclude that such activity recorded from reptiles may be considered as electrophysiological indicators of sleep. However, as in the case of mammals, such electrical brain activity is not exclusive to periods of sleep behavior and may be observed in behaviorally active animals (see, for example, [213]).

The dissociation of electrographic indices of state and behavioral indices is equally evident in the case of amphibians. On the one hand, behavioral sleep may occur in the absence of changes in brain activity. On the other hand, electrographic changes generally associated with sleep may be observed in the absence of accompanying behavioral correlates of sleep, such as increased arousal threshold [78].

All of these examples serve to emphasize that without simultaneous behavioral observations, electrographic recordings in a wide range of animal species may be of limited value in the examination of sleep duration. By the same token, behavioral characterization of sleep in the absence of electrographic correlates may also lead to unreliable sleep

length values, since the criteria for defining behavioral sleep are often inconsistently and unreliably applied.

While many fish and invertebrates show behaviors typically associated with sleep in mammals, systematic verification of the presence of all components of behavioral sleep is lacking. Further, the absence of neuronal substrates required to generate electrographic changes comparable to those observed in mammals makes it necessary to establish alternative indices of neuronal activity to indicate sleep or rest. The feasibility of such methodology has been shown by Kaiser and Steiner-Kaiser [92] who demonstrated an association between electrographic changes in certain neuronal groups and alterations in behavioral responsiveness in forager bees (see page 273).

To summarize, the approach to the study of the evolution of sleep has been strongly influenced by an all but exclusive dependence on electrophysiological criteria of sleep which were initially developed as a means of defining sleep in mammalian species. Reliance on such a circumscribed set of indices to define sleep across phylogeny may sometimes result in the misidentification of sleep and waking states in mammals and birds, and is almost always problematic when applied to the study of sleep in non-mammals.

It would seem essential, therefore, that electrographic measures always be interpreted within the framework of behavioral appraisal. Furthermore, it is essential that definitions of sleep in non-mammalian species be determined initially on the basis of behavioral manifestations of that state, and subsequently correlated with electrographic indices which take into consideration the differences in structure and function between the nervous systems of these species and those of mammals.

Drowsiness

An additional problem in the definition of sleep arises relative to intermediate or transitional states, which are generally referred to as "drowsiness," "light-sleep" (e.g., [24]), or "quiet wakefulness" (e.g., [53]).

The state of drowsiness may be generally defined as an intermediary state between active wakefulness and sleep which is characterized by behavioral quiescence, but during which the arousal threshold remains low. Such a state is considered to be the "most common pattern of cortical activity during waking in domestic animals" [152], especially in domestic herbivores, and comprises a large percentage of the waking state in dogs and cats. In addition, drowsiness has been reported in such diverse species as tapirs, sloths, rhesus monkeys, shrews, moles, hedgehogs, and opossums.

In most mammals this state is accompanied by an increase in slow wave activity in the EEG. In birds, drowsiness is generally characterized by bursts of slow wave, high amplitude EEG activity on a background of low amplitude, fast activity [129, 148, 207, 225]. In reptiles, a transitional state typically referred to as quiet wakefulness (QW) is characterized by high amplitude, arrhythmic spikes. Quiet wakefulness and sleep are differentiated primarily on the basis of the frequency with which such spiking occurs. QW comprises a large percentage of the 24-hr day in most reptiles and can sometimes continue for as long as several days [53,60].

Despite numerous discussions of the problem (see, for example, Symposium discussion [43]) there are no standardized procedures regarding the differentiation between sleep and these intermediate states, nor is there general agreement concerning the desirability of including such states in the

measurement of sleep length. Clearly, the decision to include or exclude drowsiness in sleep duration measures could result in drastically different values. As such, it is important to consider the manner in which such decisions were made when comparing sleep durations of different species. Difficulties in the definition and classification of intermediate states may also account for some discrepancies, across studies, in the reported sleep durations of a given species.

Because of the problems involved in the definition of sleep, especially with regard to non-mammals, some authors have chosen to employ the more conservative term of rest. When the behaviors which are termed "rest" in these studies meet the previously described criteria for behavioral sleep, we have chosen to include these rest times in the following section and in the table.

INVERTEBRATES

Little attention has focussed specifically on sleep in invertebrates. It is well documented that many invertebrate species, especially insects, exhibit a rest-activity rhythm dependent upon photoperiod and light intensity [163]. The rest phase is often characterized by prolonged episodes of immobility. Studies involving invertebrates have been almost exclusively concerned with the activity portion of the cycle. Few authors have observed and analyzed behavior during rest, thus it is by no means established that sleep is even present in invertebrates.

Yet, the finding of compensation of rest after rest deprivation in cockroaches would imply a process similar to mammalian sleep [192]. In addition, electrophysiological studies in arthropods have demonstrated a circadian modulation in excitability of both central and peripheral components of the visual system [14, 15, 21]. Similarly, Kaiser and Steiner-Kaiser [92] have reported a circadian pattern of spontaneous firing of optomotor interneurons in the forager bee, *Apis mellifica carnea*, maintained in constant darkness. In addition, these neurons exhibited a circadian variation of firing in response to moving stimuli, reflecting an oscillation in sensitivity. An arousal stimulus, consisting of a single air puff, during the trough of neuron sensitivity changed the state of the optoneuron so that it subsequently reacted to a visual stimulus. These findings indicate that the neuronal phenomena may be correlates of the bee's circadian sleep-wakefulness rhythm. Further studies are needed to clarify the possible relationships between these oscillations in sensitivity and the circadian rest-activity cycle.

In the absence of more extensive electrographic data, the term "sleep," as applied to insects, has traditionally been defined in a confusing and ambiguous way. For example, Rau [140] makes no distinction between sleep and tonic immobility. On the other hand, several authors (see, for example, [12, 147, 220]) use 'akinesis' and 'sleep' synonymously, and differentiate these terms from 'tonic immobility' which, in contrast to 'sleep' or 'akinesis,' is *intensified* by tactile stimulation. Akinesis has been defined as inactivity due to physiological and central nervous stability, with the implication that intensification in stimulation will cause instability and consequent activity [12]. These criteria are in accordance with those postulated by Kleitman [102] for sleep, a decrease or cessation of muscular activity and a raised threshold of reflex excitability. Applying Flanigan's [52] conceptualization of behavioral sleep, it appears that at least some invertebrate species do exhibit sleep behavior.

The behavior of 26 cockroaches, *Leucophaea maderae*, was continuously examined for 2-5 days under a 12L/12Dim

photoperiod. These insects exhibited rest times which comprised an average of 58.3% (14 hr) of the 24-hr day. Rest time was slightly weighted toward placement within the light period [191].

Typical "sleep postures" and "sleeping sites" have been described for the *Aplysia*, a marine mollusc, and for many insects [50, 138, 140, 141, 166, 177, 222]. Furthermore, specific postures have been found to be associated with an elevated arousal threshold in the *octopus vulgaris* ([108]; cited by [90]) and in many insects [35, 36, 37, 73].

Quantitative measures of arousal thresholds during different rest postures suggest the existence of an intensity factor of sleep in moths. For example, Andersen [12] was able to lift the wing of the insect with a fine brush and allow it to drop without eliciting behavioral arousal.

In summary, the presence of sleep among insects remains highly debatable. Nevertheless, if we wish to understand sleep in its most evolved form, i.e., in mammals, we must study its evolution by tracing sleep-like behaviors in invertebrates, as well. Additional studies designed to specifically and critically examine the inactivity phase of the rest-activity cycles of various species will provide the basis for an evolutionary approach to sleep.

Fish

Probably due to the difficulty of electrographic recording in a water medium the number of studies concerned specifically with sleep duration in fish is small. Though many authors have described the rest-activity patterns and resting behaviors of various species, reports generally consist of direct observations during an unspecified portion of the 24-hr day. Such studies have yielded little quantitative data.

Spencer [171] continuously recorded the activity of 10 species of freshwater fish for up to several days at a time. On the basis of these data the author concluded that some of the fish showed a fairly continuous 24-hr pattern of activity while others exhibited a monophasic rest-activity pattern. Behavior during rest was not described.

Weber [219] described the resting niches, postures, changes in color, breathing frequencies and sensitivity to stimulation of 200 species of fish observed in various aquaria. The duration of sleep periods was not measured. However, it was reported that some species exhibited only very short periods of rest while others were constantly active (e.g., dogshark, *Galeorhinus canis*; tunafish, *Thunnus thynnus*; mackerel, *Scamber scombrus*; swordfish, *Osteoglossum bicirrhosum*; and two species of sturgeons, *Acipenser sturio* and *A. ruthenus*). It remains to be determined if these species are capable of obtaining sleep while swimming. However, such behavior is well documented in some aquatic mammals (see pp. 282).

Starck and Davis [174] investigated the nocturnal habits of approximately 150 species of reef fish. Although they did not specifically address the question of sleep duration, they described several indices of behavioral sleep. One example was the formation of a mucous cocoon in which parrot fish remained inactive throughout the night. An extensive description of the secretion of the mucous envelope by these fish is given by Winn [221].

Tauber and Weitzman [187] described in more detail the behavioral and physiological changes which occurred during the rest-activity cycle in two families of reef fish including one species of wrass (slippery dick, *Irideo bivittata*) and 8 species of parrot fish (*Scaridae*). All species observed

showed unambiguous behavioral sleep. Sleep durations were not reported, since the fish were only observed in periodic, two-hour intervals during the night. In addition, Tauber [183] confirmed behavioral sleep in several further species.

The distribution of motor activity and rest in 6 species of fish housed in an aquarium was studied by Karmanova *et al.* [97] using a sampling procedure which recorded activity levels at various times during the 24-hr day. Spiny dogfish, *Squalus acanthias*, and brown meagres, *Sciaena umbra*, were constantly active. Stingrays, *Dasyatis pastinaca*, and mullets, *Mugil sp.*, exhibited a nocturnal placement of rest while sea nallim, *Gaidropsaurus mediterraneus*, and rascasses, *Scorpaena porcus*, showed diurnal sleep placement. Sleep was identified by registration of motor activity, respiration, heart rate and arousal thresholds, which were measured by reaction to sound, light and tactile stimuli. Sleep duration was not reported.

Siegmund [168] continuously measured locomotor activity and resting habits of three species of European freshwater fish. The fish were kept in aquaria under natural lighting conditions and were recorded for periods of 10 days to 1 month at several times during the year. Duration of rest in 10 perch, *Perca fluviatilis*, depended on the season and varied between 5 hr and 10 hr. All rest occurred at night. In contrast, an unspecified number of tench, *Tinca tinca L.*, exhibited rest periods during the day, interrupted by only brief episodes of movement. Again duration of rest varied from 4 hr to 15 hr, depending on the season.

Red-eye, *Scardinius erythrophthalmus L.*, were active during daytime and rested for only short periods at night. The 1–3 hr rest per 24 hr were often characterized by only a diminution of activity. The rest-activity pattern virtually disappeared during winter with winter values of activity being over four times lower than summer activity measures.

Shapiro and Hepburn [165] observed the sleep behavior of 30 fish, *Tilapia mossambica*, after adaption to a 15L/9Dim photoperiod. After a 90 minute (± 30 minutes) sleep onset period, 80% of the fish slept for 6.5 to 7.5 hr (27–31.3% of 24 hr). Sleep was defined by an increased threshold of response to electrical and feeding stimuli. Under a 12L/12Dim photoperiod, sleep length increased by approximately 3 hr (41.7% of 24 hr). When fish were exposed to 96 hr of continuous light, no sleep behavior was observed. On termination of the light phase, sleep onset latency was substantially reduced (to 30 ± 15 min) suggesting a behavioral response to sleep deprivation.

Only 2 studies concerned with sleep in fish have included EEG recordings. Peyrethon and Dusan-Peyrethon [134] continuously recorded 25 tenches, *Tinca tinca*, for several days under a 12L/12D photoperiod. No differences in cerebral activity between states of behavioral activity and rest were found. Individual behavioral rest episodes lasted for 10 to 20 min. Total rest time comprised 80% (9.6 hr) of the light period, 40% (4.8 hr) of the dark period. Under continuous illumination, rest comprised 75% (9 hr) of former daytime and 73.8% (8.9 hr) of former night hours.

Recently, Karmanova [94] and Karmanova and Lazarev [96] have obtained polygraphic EEG and EMG recordings from catfish (brown bullhead, *Ictalurus nebulosus*). Spectral analysis of short EEG fragments revealed a predominance of power in the low frequencies during waking. During behavioral sleep lower frequencies dominated. Since recordings were made only during intervals of unspecified duration during the 24 hr, total sleep time could not be assessed.

The attempts to decide the question of the presence of sleep in fish on the basis of brain activity recordings have not been successful. Many species undoubtedly exhibit behavioral indices of sleep. Yet, quantitative data on behavioral response thresholds, as well as rapid state reversibility, are lacking. Polygraphic recordings must be extended to many more species before any generalization can be made concerning brain activity during behavioral sleep in this class.

Amphibians

Literature specifically delineating the sleep durations of amphibian species is also scarce. Therefore, as with invertebrates and fish, we have chosen to include in the following discussion several studies which refer more generally to rest time.

Hobson [79] and Hobson, Goin and Goin [80,81] observed the field behavior of two species of tree frogs, *Hyla squirella* and *Hyla cinerea*, and the behavior of a third species of tree frog, *Hyla septentrionalis* in the laboratory. While the field behavior of all three species is reported to be similar, marked differences were noted between *H. squirella* and *H. cinerea*, on the one hand, and *H. septentrionalis* on the other. In the field, specimens (about 20 of each species) were nocturnally active and were found to be "resting during the day." The resting state was reversed by moderately intense stimulation, and in the authors' view could be considered as "sleep." The behavior of *H. septentrionalis*, observed in the laboratory, at temperatures of 20°C to 21°C, and under natural lighting conditions, consisted of continuous sleep.

Specimens of all three species were electrographically recorded in the laboratory for 24-hr periods for up to three consecutive days. Electrographic changes were noted in association with behavioral sleep, consisting of *increased* frequency and *decreased* amplitude in the frontal EEG. During intervals characterized by such EEG activity, changes in illumination and hand-claps were sometimes without effect in arousing the animals. Arousal threshold was not systematically measured, however.

Hobson [78] also studied 10 adult bullfrogs, *Rana catesbiana*, eight of which were recorded electrographically. Behavior was observed, and arousal threshold was measured, in two frogs not implanted with electrodes. Quiet waking in bullfrogs was accompanied by changes in the EEG similar to those found to accompany sleep in the tree frogs. However, in the bullfrogs, no decline in responsiveness to electrical stimulation was observed. On the basis of this evidence, the author concluded that *R. catesbiana* did not sleep.

Karmanova and Lazarev [96] examined grass, or brown frogs, *Rana temporaria*, by means of behavioral observation and EEG. These animals exhibited sleep-like states (SLSs) which could be divided into three categories based on degree of muscle tone and responsivity. All sleep-like states were characterized by decreased muscle tone relative to waking, typical postures, loss of alertness, and marked bradycardia. In addition, the deepest SLS (SLS-3) was accompanied by a slight enhancement in slow wave activity in the EEG. No estimates of sleep duration were reported.

Karmanova [94] also studied 6 lake frogs, *Rana ridibunda*, over several 24-hr periods. Sleep-like states were found to occupy 80–90% of the 24-hr day. However, only SLS-3, which comprised 10% (2.4 hr) of the 24-hr day, was characterized by diminished levels of alertness.

The most precise delineation of sleep duration in amphibians was provided by Huntley *et al.* [83], who investigated behavioral and electrophysiological correlates of the rest-

activity cycle of the Western toad, *Bufo boreas*, for two 24-hr periods. Under a natural light cycle, these animals were found to rest about 87% of the light period and 24% of the dark period (14.6 hr per 24 hr, assuming 14L/10D photoperiod). During the light period, rest period length averaged 25 ± 15 min, interrupted by brief awakenings, assumed to be related to a "defense alerting system." While the authors typically referred to the periods of inactivity as rest, such events did meet the criteria for behavioral sleep. Behavioral sleep in *Bufo boreas* was accompanied by a slowing of brain activity.

The behavior and EEGs of 21 tiger salamanders, *Ambystoma tigrinum*, have been examined by Lucas *et al.* [116] and McGinty [118]. Sleep duration was not considered in this study, although presence of a 4-hr ultradian rest-activity cycle was established. The cycle was observed across the 24-hr day and did not show seasonal variations, leading the authors to infer an endogenous controlling mechanism for the rhythm. Behavioral rest in this species was accompanied by changes in EEG frequency similar to those seen in "homologous mammalian neural tissue."

Himstedt [76] measured rest and activity in the smooth newt, *Triturus vulgaris* L., under laboratory conditions with simulated natural lighting. These animals were reported to rest during the day and were most active at dawn and dusk (crepuscular). Depending on the season, the habitats of these animals changed. During spring the primary habitat was aquatic, in summer it was terrestrial. Dramatic alterations in rest duration accompanied these changes in habitat. In water, 4.6 hr per 24 hr were spent resting. On land, 11 hr per 24 hr were comprised of rest.

To summarize, the nine species of amphibians studied have all exhibited periods of behavioral rest, typically of durations in excess of 50% of the 24-hr day. All studies in which electrographic measures have been examined have reported changes in brain electrical activity which accompany such resting states, although the form of the reported changes is not consistent. Further, while these resting states are generally characterized by decreased responsiveness to external stimulation, at least one species, *R. catesbiana*, retains a level of responsiveness equal to that observed during active wakefulness.

Reptiles

The sleep characteristics of three of the four orders of living reptiles have been investigated, at least to some extent. Studies have been conducted on chelonians (turtles and tortoises), crocodylians (crocodiles, alligators and relatives), and squamata (lizards and snakes). The remaining order is comprised of only one species, the tuatara, *sphenodon*, an iguana-like reptile confined to certain islets near the coast of New Zealand.

At least one author [210] suggests that reptiles "possess a mammalian type of sleep for the first time in phylogeny and there is a qualitative difference between this type of 'real' sleep and the ubiquitous resting state" of fish and amphibians (p. 273-274). While it appears that virtually all reptiles exhibit behavioral sleep states, results vary widely with regard to the associated EEG characteristics and the mammal-like nature of these states [59, 70, 213].

Measures of sleep length have been reported for four species of chelonians. In addition, two species of chelonians have been reported not to sleep. Flanigan *et al.* [59] examined sleep and wakefulness in 11 North American box turtles, *Terrapene carolina*, under conditions of continuous il-

lumination and temperature (26°-29°C). Two recording times were used (either 12-13 hr or 24 hr/day) for 7 to 9 consecutive days. Behavioral sleep was found to occupy between 79% and 91% of total recording time (19 to 21.8 hr per 24 hr).

Six red-footed tortoises, *Geochelone carbonaria*, examined under the same conditions, were reported to exhibit unambiguous behavioral sleep comprising 88% to 94% of the 12 to 13 hr recording sessions [54]. In both of these species, behavioral sleep was accompanied by EEG spikes which disappeared with induced or spontaneous arousals.

Investigations of the sleep of European pond turtles, *Emys orbicularis*, revealed sleep periods of substantially shorter duration, comprising only 29% (6.9 hr) of the 24-hr recording period [95].

Hermann *et al.* [75] electrographically studied the margined tortoise, *Testudo marginata* Schopfer, and reported that 48% (11.5 hr) of the 24-hr day was spent asleep.

Susic [180], using 24-hr EEG recordings and 3-hr observation periods, found no evidence for the presence of sleep in three sea turtles, *Caretta caretta* L. Under conditions of continuous light (reduced at night), this species exhibited an alternation between periods of activity and inactivity which were not accompanied by changes in level of responsiveness to light stimuli.

Similarly, Walker and Berger [213] concluded that seven adult tortoises, *Testudo denticulata*, did not sleep during continuous 24-hr EEG recording and observation periods (12L/12D), lasting for up to three weeks. While these investigators found electrographic changes, in the form of increased spiking activity, to accompany periods of quiet waking, such activity was not specific to periods of rest. In addition, no changes in responsiveness to electric shocks were observed during periods of increased spiking activity.

There are only two reports specifically addressing sleep duration in crocodylians. Meglasson and Huggins [120], employing electrographic and behavioral criteria and 24-hr recording periods (12L/12D), found quiet sleep to occupy 12.7% (3 hr) of the 24-hr period in five young (4-6 months) caimans, *Caiman sclerops*. An average of 11 ± 2.6 sleep episodes occurred per 24 hr and were most frequent between 0200 hr and 0600 hr.

Flanigan *et al.* [60] also studied *Caiman sclerops*, both behaviorally and electrographically. While no specific sleep duration measures were given by these authors, it was reported that the ten adult (approximately 2-5 years) specimens spent 50% of the recording time (6 to 12 days) in Postures 3 and 4. Both of these postures were considered by the authors to meet criteria defining sleep. In both studies, behavioral sleep was associated with spiking activity in the EEG.

Peyrethon and Dusan-Peyrethon [134] recorded brain electrical activity from one caiman, *Caiman latirostris*, continuously for one month. Sleep duration was reported to be 12.5 hr per 24 hr, 1% of which was considered to be active sleep.

Van Twyver [203] studied seven alligators, *Alligator mississippiensis*, electrographically and behaviorally for up to three months. Initial changes in EEG were found to be associated with changes in ambient temperature. When temperature was controlled, the author found no evidence of sleep in this species.

Saurians and serpents comprise the last group of reptiles to be considered here. Sleep durations of three species of Iguanid lizards have been reported [53, 84, 184]. Because these reptiles are of sufficient size to allow extensive elec-

trode placements within the brain, they have been the preferred experimental preparation within the saurian group.

Tauber *et al.* [183] conducted observational and electrographic investigations of the sleep of 23 adult lizards, *Ctenosaura pectinata*, and found sleep durations of 6 to 9 hr, always occurring during the night. However, since daytime recordings were restricted to 2 to 3 hr, 24-hr sleep durations could not be determined.

Flanigan [53], also using 12-hr recording periods, across 7 to 11 consecutive days, recorded the sleep and wakefulness of three black, *Ctenosaura pectinata*, and three green, *Iguana iguana*, lizards of unknown age. In addition to EEG recordings, time-lapse video was employed to obtain behavioral data. Animals were maintained on a 12L/12Dim cycle, with lighting at night only of sufficient intensity to allow observation and photography. Behavioral response latencies to electric shock were also measured. As in the caiman, these animals exhibited four behavioral postures, Postures 3 and 4 meeting behavioral criteria for sleep. These postures comprised 34.8% to 66.5% (4.2 hr to 7.9 hr) of total recording time. The EEG during these intervals was characterized by slight declines in frequency and substantially diminished amplitudes.

Huntley *et al.* [84] electrographically recorded the sleep of 8 desert iguanas, *Dipsosaurus dorsalis*, for two 12-hr or 24-hr periods. A 12L/12D photoperiod was maintained. Sleep comprised 68% to 74% (16.3 hr to 17.8 hr) of the 24 hr. The sleep EEG in this species was also characterized by reduced frequency and amplitude relative to waking.

The sleep of two species of chameleons, *Chameleo jacksoni* and *Chameleo melleri*, has been examined [185]. While the primary aim of this study was to examine eye movements during selected 2 to 3-hr periods of sleep, the authors state that two specimens of each species appeared to sleep "throughout the night" unless disturbed. Sleep was accompanied by changes in the EEG relative to waking, and consisted of a general slowing, with bursts of high-voltage spikes.

Romo *et al.* [149] studied the sleep of 13 horned lizards, *Phrinosoma regali*, under conditions of stable temperature ($30 \pm 0.5^\circ\text{C}$) and a 12L/12D cycle. The EEG of each animal was recorded during two sessions of 24 hr each. The authors reported behavioral sleep accompanied by both increased delta activity (slow wave sleep) and by low voltage fast activity (fast wave sleep). Sleep was found to be monophasic and nocturnally placed, with SWS being initiated at around 1800 hr and continuing for 6.4 ± 0.2 hr. Fast wave sleep was initiated at around midnight and continued for 5.9 ± 0.4 hr (12.3 hr per 24 hr).

The sleep of only one serpente has been examined. Peyrethon and Dusan-Peyrethon [135] electrographically recorded one python, *Python sebae*, continuously over several 24-hr periods. Photoperiod was unspecified. Sleep duration ranged from 65% of the 24 hr (15.6 hr) when the animal was hungry to 85% of the 24 hr (20.4 hr) of the 24 hr after being fed.

To summarize, of 16 species of reptiles studied, 13 have been reported to exhibit unambiguous behavioral sleep, with durations ranging from 3 hr to 22 hr per day. During behavioral sleep, all of these species exhibited changes in brain activity, as well. In general, such changes were characterized by an overall reduction in frequency and amplitude, with superimposed spiking activity frequently reported.

In the three species which were reported not to sleep, lack of electrographic changes and/or lack of change in

arousal threshold comprised the basis on which the decision was made regarding the absence of sleep. In light of the fact that only three of the 16 species studied exhibited no sleep additional examinations of these species would be desirable.

Birds

Resting postures in numerous species of birds have been described [74, 85, 103]. Stiefel [176] compiled rest and sleep behaviors of approximately 400 bird species. Because of the uncertainty and inconsistency with which behavioral indices of sleep have been applied in birds [10] we have chosen to discuss in this section only those studies which verified behavioral measures with polygraphic recordings. However, in the interest of completeness we have also chosen to present sleep length data on 31 additional species of wild birds in the table (from [10]).

Since the first electrographic study in birds by Klein *et al.* [101] sleep durations of only about a dozen of the 8600 bird species have been defined electrographically. It is generally agreed that the electrographic indicators of sleep in birds are essentially the same as those in mammals. Active sleep, however, is typically of only short duration (on the order of seconds) and is not always accompanied by muscle atonia. A notable exception is the goose [48]. In addition, it has been reported that slow wave activity may occur during waking in at least three species [148, 194, 206, 225].

Using 1-hr sampling across 24-hr periods and simulated natural photoperiod, Karmanova and Churnosov [95] found that 17 adult White Leghorn hens, *Gallus domesticus*, slept 49% (11.7 hr) of the 24-hr day. It should be noted that these authors made a distinction between telencephalic (44%) and rhombencephalic (5%) sleep on the one hand, and cataleptic immobility, a sleep-like state comprising an additional 18% of the 24-hr day, on the other hand.

Hishikawa *et al.* [77] studied the EEG characteristics of sleep in 11 young chickens (8–15 days) and made behavioral observations on 39 more. Using 2-hr to 10-hr recording sessions (mean=5.2 hr) under conditions of constant dim illumination, the authors found sleep to occupy $73.5 \pm 12.1\%$ of the recording time.

Sleep durations in two species of waterfowl have been reported.

Dewasmes *et al.* [48] studied the sleep characteristics of 4 adult geese, *Anser anser*, of the "landaise" strain before, during and after a 40-day period of fasting. Using continuous recordings for 3–4 days under 12L/12D conditions, the authors found sleep to occupy 25.8% of 24 hr (6.2 hr). They distinguished a state of drowsiness which comprised 32.7% (7.9 hr) of 24 hr. The proportion of PS and SWS was only slightly higher during the night than during the day, while drowsiness was evenly distributed.

Four domestic ducks, *Anas platyrhynchos domesticus*, were electrographically recorded for up to 120 hr under simulated natural lighting conditions (11L/11D, 2 dim for dawn and dusk) [225]. In addition, observational data were collected periodically, including time-lapse video photography for a total of 16 24-hr sessions. Daily sleep amounts averaged 10.8 hr, distributed evenly across the photoperiod. Similar to the findings in falconiformes, the authors reported the presence of slow wave EEG activity during relaxed waking.

Rojas-Ramirez and Tauber [148] have reported on the sleep of two species of avian predator. The sleep behaviors and EEGs of two birds, a hawk, *Buteo jamaicensis arborealis*, and a falcon, *Herpetotheres cachinnans chapmani*, were quite similar, with sleep length comprising

about 4 to 5 hr of the 24-hr recording sessions. The sleep pattern for both birds was nocturnal, with periods of sleep ranging from 3 to 40 min with interruptions of wakefulness for periods of 5 to 10 min. Slow wave activity in the EEG typical of sleep was also observed during periods of waking in both birds.

Stahel *et al.* [173] measured sleep duration in 5 little penguins, *Eudyptula minor*, by continuous polygraphic EEG recording for 4 hr during dim and 4 hr during light. The birds were kept under a light/dim red photoperiod (hours unspecified). Sleep comprised 68.9% of recording time (26.9% during light and 42.0% during dim). Calculated for 24 hr, sleep comprised 8.27 hr (assuming 12L/12D photoperiod).

Sleep was electrographically recorded in four Emperor penguins, *Aptenodytes forsteri*, under natural conditions for continuous 24-hr periods (Dewasmes, Le Maho and Buchet, personal communication). Sleep comprised 44.5% (10.7 hr) of recording time, with individual sleep episodes averaging 4.7–5 min. Sleep episodes occurred during light and darkness with distribution of sleep depending on feeding conditions.

There is close agreement among reports of sleep duration in the domestic pigeon, *Columba livia*. Van Twyver and Allison [206] examined sleep in 8 adult pigeons using EEG and visual observation. The 24-hr recordings in a 12L/12Dim photoperiod (with constant dim red illumination) revealed average total sleep time of 10.6 hr (44.3%). Mean sleep period length was 7 min. Sleep was characterized by diminished responsiveness to electric shock, compared to waking.

Walker and Berger [212] reported the same sleep duration of 10.8 hr per 24 hr in 3 pigeons studied behaviorally and electrographically for 24-hr periods. Both studies concluded that sleep time in this species was distributed according to illumination, with the majority of sleep (72%) [212] occurring during the dark period.

Sleep durations in the ringed turtle dove, *Streptopelia risoria*, have been reported by Walker *et al.* [215]. During two consecutive 24-hr EEG recording periods (12L/12D photoperiod), sleep comprised 85% (10.2 hr) of the 12-hr dark period. The birds presumably did not sleep during the light period. As a result of food deprivation, subcutaneous temperature in one bird was reduced from 37°C to 32.5°C. Such a decline in temperature resulted in a 10% increase in sleep time. At subcutaneous temperatures of 30°C the entire period was comprised of slow wave sleep.

Vasconcelos-Dueñas and Guerrero [209] electrographically studied the sleep of parakeets, *Aratinga canicularis*, for an unspecified duration, under constant light. Sleep comprised an average of 39% of the recording period (9.4 hr per 24 hr, assuming 24-hr recording).

The sleep characteristics of 3 species of owls have been examined. Berger and Walker [25], using electrographic and behavioral measures, including acoustic arousal threshold, determined that burrowing owls, *Speotyto cunicularia hypugaea*, spent 59.5% (14.3 hr) of the 24-hr recording period asleep. Although 3 of the 4 birds studied slept slightly more during the 12-hr light period than during the 12 hr of darkness, there was no substantial diurnal placement, “. . . in that sleep occurred extensively during both day and night.”

Two tawny owls, *Strix aluco*, were studied behaviorally and electrographically by Susic and Kovacevic [181]. The two birds were found to exhibit sleep durations similar to those reported for the burrowing owls: 66.7% (16.0 hr) of the

24-hr recording sessions were spent asleep, with sleep time evenly distributed across a 12L/12D photoperiod. While drowsiness does not appear to be included in this figure, another report, presumably on the same birds [93], gives identical slow wave sleep times (15.5 hr) and does include drowsiness.

Karmanova and Churnosov (in [94]) studied 2 species of owl, the tawny and the polar white owl (snow owl), *Nyctea scandiaca*, electrographically. In contrast to the findings of Susic, these authors reported sleep in the tawny owl to comprise only 28.2% (6.8 hr) of the 24-hr recording period. However, as with chickens, these authors differentiated between sleep and cataleptic immobility, on the basis of EEG measures. This state, which occurred only during the day, comprised 25% of the 24-hr period. Like sleep, cataleptic immobility was characterized by elevated arousal threshold.

The polar white owl was reported to sleep 33.2% (7.9 hr) per 24-hr period. Cataleptic immobility accounted for another 7 hr of each 24 hr.

The sleep profiles of six adult starlings, *Sturnus vulgaris*, were examined by Tymicz *et al.* [195]. Because these birds were observed to be continuously active during the day, EEG recordings were made only at night (natural or 12L/12D photoperiod). Total sleep time comprised 39% to 41% of the recording period (4.7–4.9 hr). The difference in amount of total sleep resulted from seasonal changes in paradoxical sleep amounts.

Tymicz *et al.* [195] studied five chaffinches, *Fringilla coelebs*, under the same conditions. Approximately 58% (7.3 hr) of the recording period was spent in sleep.

Because electrophysiological indicators of sleep in birds are essentially the same as in mammals, sleep duration measures in these species may be more reliable than those reported for amphibians and reptiles. However, in most cases the number of animals used has been quite limited, perhaps restricting the generalizability of results. Nevertheless, it is clear that all birds thus far studied exhibit behavioral and electrographic sleep, ranging in duration from 4 hr to 16 hr per day.

Mammals

The data concerning the sleep duration of mammals are relatively extensive. Zepelin and Rechtschaffen [224] reported on the sleep lengths of 53 mammalian species, and in the past 10 years the sleep characteristics of several additional species have been examined.

Monotremes. The phylogenetically oldest mammal for which sleep duration has been determined is the echidna or spiny anteater, *Tachyglossus aculeatus*, a representative of one of the two families of monotremes (egg-laying mammals). The only surviving member of the second family of monotremes, the platypus, has not been studied. Allison *et al.* [4] continuously recorded sleep-wakefulness patterns of five adult echidnas electrographically for up to 120 hr (mean=91 hr). Sleep was found to be distributed polyphasically with a mean sleep period duration of 27 min. Total sleep time per 24 hr was reported to be 8.6 hr. In the natural habitat, there is some evidence for a slight diurnal placement of sleep, especially during the heat of summer [69], and the most active animals studied by Allison *et al.* were also observed to sleep primarily during the day.

Marsupials. Two species of opossums have been studied, and both have been reported to have similar sleep durations. Van Twyver and Allison [205] recorded behavioral and electrographic correlates of sleep in five North American opos-

sums, *Didelphis marsupialis*. During continuous 24-hr recording periods, under conditions of constant illumination, sleep duration averaged 19.4 hr (80.8%). Individual sleep episodes averaged approximately 1 hr, with occasions of uninterrupted sleep of up to 4 hr. Though animals were recorded in continuous light, sleep was distributed relative to time of day with the major waking episode occurring between 2100 hr and 2300 hr, and intermittent activity continuing until about 0600 hr. Recordings from one animal maintained on a 9L/15D photoperiod for 48 hr revealed no differences in sleep patterns or amount.

Twenty-four hour telemetric recordings of the same species maintained on a 12L/12D photoperiod revealed slightly shorter sleep times (16.6 hr), though diurnal placement of sleep was maintained [170].

Twenty little water opossums, *Lutreolina crassicaudata*, were electrographically recorded continuously for 5 days [2]. This species was also found to sleep 80.8% (19.4 hr) of the 24-hr day.

The sleep of three additional marsupial species has been examined. Lopresti and McGinty [112] electrographically recorded sleep in three phalangers, *Trichosurus vulpecula*, and found sleep to comprise 57% (range=48% to 64%) of total recording time which was not specified.

Cicala *et al.* [42] observed the sleeping behaviors of five red kangaroos, *Megaleia rufa* (2 adults, 3 juveniles), housed at the Philadelphia Zoological Garden. Behavior was monitored on 4 days between 1000 hr and 1530 hr, considered to be the inactive period of these nocturnal animals. Sleep times ranged from 37.9% of the recording time (2.1 hr) for the youngest animal to 14.2% (0.78 hr) of recording time for one of the adults. Average sleep cycle length was 13.1 min and did not vary systematically with age.

Four adult kangaroo rats, *Potorous apicalis*, were electrographically recorded in a 12L/12D photoperiod, as well as for 3 weeks under conditions on continuous light [17]. Total sleep times comprised 48.6% (11.6 hr) per 24 hr under entrained conditions and 50.8% (12.2 hr) per 24 hr in continuous light. During the 12L/12D condition, sleep tended toward light period placement with 68% of TST occurring during that period.

A study on the same species was also conducted by Astic and Saucier [16] using animals aged 15 days to 1 month to examine states of vigilance during development in the marsupium.

Insectivores. The sleep characteristics of two species of hedgehogs have been studied. Snyder *et al.* [170] used 24-hr telemetric recordings to examine sleep in the European hedgehog, *Erinaceus europaeus*. Under a 12L/12D photoperiod, these animals were reported to sleep 14.2 hr (59%) of each 24-hr period. This value includes a "transitional state" which was characterized by intermittent spindling against a low voltage background.

Fourre *et al.* [63] also studied five European hedgehogs electrographically and reported a slightly higher sleep duration of 17.4 hr (73%) per 24 hr. Drowsiness was also included in total sleep time in this study because the authors could not reliably distinguish between this state and slow wave sleep. Sleep was weighted toward a diurnal placement.

Continuous EEG recordings for a period of one week were made on nine European hedgehogs by Toutain and Ruckebusch [193]. These authors were able to distinguish between sleep and drowsiness, and reported sleep durations of 10.1 hr (42%) per 24 hr. Drowsiness accounted for another 6 hr per 24 hr. The distribution of sleep was polyphasic and

predominantly placed diurnally. Sleep period duration averaged 17 ± 3.7 min.

Tauber *et al.* [184] recorded 24-hr EEGs in desert hedgehogs, *Paraechinus hypomelas*, and reported an average sleep duration of 10.3 hr per 24 hr. Sleep during the 12-hr interval between 1200 hr and 2400 hr accounted for 64% of total sleep time.

The sleep characteristics of two species of moles have been examined by Allison and Van Twyver [8]. Six Eastern moles, *Scalopus aquaticus*, and one star-nosed mole, *Condylura cristata*, were electrographically recorded under constant low-level illumination. Five animals were recorded continuously for 24 hr, two animals continuously for 72 hr. Behavioral observations were also made on several animals prior to implantation of electrodes. Total sleep time per 24 hr was calculated to be 8.4 hr (35%) for the Eastern moles and 10.3 hr (43%) for the star-nosed mole. A rest-activity cycle of about 4 hr was noted, although considerable variability was evident in duration of single sleep periods, ranging from 1 to 3 hr.

Godfrey [67] monitored rest-activity of eight European moles, *Talpa europaea*, in the field using radioactive labeling. Summed measures derived from 8-hr observation periods across the 24-hr day revealed an average rest time of 3.5 hr per 8 hr, or 10.5 hr per 24 hr. The longest period of rest while in the nest was 4.7 hr, the shortest was 2.2 hr. In tunnels, rest periods rarely continued for longer than 20 min.

Berger and Walker [26] made behavioral observations and continuous 24-hr electrographic recordings of sleep and waking in six adult tree shrews, *Tupaia glis*, maintained on a 12L/12D photoperiod. Attempts to measure arousal threshold were abandoned due to the inability to elicit awakenings with auditory stimuli as high as 100 dB, or, for example, by shaking animals' electrode cables. Sleep was found to occupy 65.8% (15.8 hr) of the 24-hr recording periods. This measure of sleep length includes light slow wave sleep (LSWS) which has been referred to as "drowsiness" [24].

Excluding LSWS, sleep time per 24 hr is 8.9 hr (37.1%). All animals slept more during the dark than during the light period.

Three additional species of shrews were examined by Allison *et al.* [6]. Three lesser short-tailed shrews, *Cryptotis parva*, were observed continuously for 24-hr periods, two under constant low-level illumination and one in 12-hr low-level white light/12-hr low-level red light. Total sleep time was 9.1 hr (38%) per 24 hr. All three animals exhibited polyphasic sleep patterns. Under constant illumination, sleep was distributed evenly across 12-hr periods; in the 12 hr white/12 hr red condition, 65% of total sleep time occurred during the white light period.

One greater short-tailed shrew, *Blarina brevicauda*, was studied under the same conditions (constant illumination) and was found to sleep 62.4% (14.9 hr) of the 24-hr observation period. In an earlier study, Van Twyver and Allison [204] had failed to find any "convincing sign of slow wave and paradoxical sleep" during 24-hr electrographic recordings of two animals, despite a 15-day adaptation period.

The third species of shrew studied by Allison *et al.* [6] was the musk shrew, *Suncus murinus*. Seven animals were electrographically recorded under constant low-level illumination for at least 24 continuous hours. Behavioral observations were also made. Sleep was found to comprise 12.8 hr per 24-hr recording period. Sleep occurred throughout the 24 hr.

Rest time has been reported in three species of British

shrew. Crowcroft [44] recorded rest and activity patterns in four common shrews, *Sorex araneus*, two Pygmy shrews, *Sorex minutus*, and one water shrew, *Neomys fodiens*, continuously for at least eight 24-hr periods. Animals were maintained on a 12L/12D photoperiod. Rest times correspond with sleep durations in other species: 7.8 hr per 24 hr (32.4%) in the common shrew, 8.5 hr per 24 hr (35.6%) in the Pygmy shrew, and 13.6 hr per 24 hr (56.8%) in the water shrew.

Finally, the tenrec, *Centetes ecaudatus*, an insectivore native to Madagascar, was electrographically recorded by means of telemetry over several 24-hr periods [170]. Sleep, including a "transitional state," comprised 65% (15.6 hr) of the 24-hr period (12L/12D).

Chiroptera. The study of sleep duration in this order has been confined to two species of the Vespertilionidae family, the little brown bat, *Myotis lucifugus*, and the big brown bat, *Eptesicus fuscus*. The little brown bat was electrographically recorded during exposure to ambient temperatures between 33°C and 5°C. At 33°C sleep comprised 83% of total recording time (19.9 hr per 24 hr), at 26°C total sleep declined to 46% of recording time (11 hr per 24 hr). Between 19°C and 21°C total sleep increased to comprise 74% of recording time (17.8 hr per 24 hr). Below 19°C sleep was replaced by a "unique state of consciousness" [41].

The big brown bat was reported to sleep 19.5 hr per 24 hr [224].

Primates. Four species of primates in which sleep has been studied belong to the suborder Prosimia, one loris, one galago and two lemurs.

Six slow lorises, *Nycticebus coucang*, were observed for a total of 72 hr (3 hr observation for each hour of the day) while individually caged and exposed to the natural light-dark cycle [188]. During observation periods, day or night, a 5 watt red light illuminated the cage. Sleep was monophasic and occurred between 0600 hr and 1700 hr (11 hr per 24 hr). Animals slept in a sitting attitude 78% of the time and in a lying-down posture 22% of the time.

The sleep EEGs of 15 bushbabies, *Galago senegalensis*, were examined by Bert *et al.* [30], during five consecutive recording sessions of 6–8 hr each. Recorded in darkness, while in restraining chairs, animals averaged 97.6% (7.8 hr) of the period in sleep. Recorded in constant light, total sleep time averaged 7.6 hr (95.5%).

Due to the difficulty in obtaining this species, Vuillon-Cacciuttolo *et al.* [211] electrographically studied the sleep of one lemur, *Lemur macaco fulvus*, over a 24-hr recording period using telemetry. The animal slept 39% (9.5 hr) of the recording period with sleep placed primarily within 2 intervals, 2000 hr–0400 hr and 1100 hr–1400 hr. Average sleep episode length was 3.3 hr. The photoperiod was unspecified.

Pariente [130] observed the behavior of an unspecified number of malagasy Lemurs, *Phaner furcifer*, for one year in their natural environment. The animals were strictly nocturnal, emergence from the nest occurred when the level of light was sufficiently low (1745 hr–1900 hr), and return to the nest as soon as the light level increased (0500 hr–0600 hr). Time in the nest thus varied with the season, total sleep time was about 11–12 hr.

The majority of primate species studied (13) belong to the suborder Anthropoidea.

Three adult owl monkeys, *Aotus trivirgatus*, were electrographically recorded during a minimum of two 24-hr periods using a 12L/12Dim photoperiod [133]. Cable recordings were carried out in unrestrained animals. Sleep occupied 85.6% (10.3 hr) of the light period and 55.8% (6.7 hr) of

the dim period, for a total sleep time of 17 hr per 24 hr (70.8%). Mean total sleep time declined to 14.7 hr per 24 hr as an immediate result of 180-degree reversal of the light-dim cycle.

Adam and Barratt [1] studied three adult squirrel monkeys, *Saimiri sciureus*, using 12-hr electrographic recordings (sampling, 5 min per 15 min) during the normal dark cycle (12L/12D) of the colony room for 7 consecutive nights. Twenty-four-hour data recorded from two of the animals indicated no sleep during the light period. Monkeys were confined in restraining chairs during sleep recordings. Sleep occupied 82.4% (9.9 hr) of the recording period.

The EEG sleep of four patas monkeys, *Erythrocebus patas*, and four vervets, or African green monkeys, *Cercopithecus aethiops sabaues*, were examined by Bert and Pegram [32] for a total of 10 nights (13.5-hr recording sessions) and 8 nights respectively. During recordings, monkeys were confined in restraining chairs. Patas monkeys slept for an average of 80.4% (10.8 hr) of recording time and vervets spent an average of 76.6% (10.3 hr) of recording time asleep.

Balzamo *et al.* [20] studied seven African green monkeys (3 adults, 3 subadults and 1 juvenile) electrographically during 2 to 7 12-hr dark periods. Total sleep time for this group was reported to be 10.1 hr. Again, animals were seated in restraining chairs during recordings.

Sleep duration in rhesus monkeys, *Macaca mulatta*, has been studied by several groups. Kripke *et al.* [108] recorded the sleep EEGs of 10 monkeys (2.7–5 years) over a total of 71 nocturnal periods (mean duration=7.8 hr). Sleep occupied 80% (6.2 hr) of the recording periods, including drowsiness. Monkeys were seated in restraining chairs.

Bert *et al.* [31] studied 12 rhesus monkeys (2–4 years) recorded electrographically during a minimum of 5 nights (2200 hr to 0600 hr) while seated in restraining chairs. Sleep was found to occupy 88.7% (7.1 hr) of the recording period.

Crowley *et al.* [45] electrographically recorded sleep in 34 rhesus monkeys over 24 hr. A 12L/12D photoperiod was used and monkeys were loosely restrained by a metal neck ring. Under these conditions, sleep comprised 49% (11.8 hr) of the 24-hr period. Frequent daytime napping was observed.

Swett [178] also observed napping in 16 rhesus monkeys in a natural environment, with sleep comprising 6% (0.5 hr) of 8-hr observation periods (0800 hr to 1600 hr).

Six adult pigtail macaque monkeys, *Macaca nemestrina*, were electrographically studied for a total of 20 14.5-hr recording sessions (1700 hr to 0730 hr) [143]. Monkeys were also constantly monitored on closed-circuit TV. Total sleep times from two nights for each animal were used to determine average sleep duration. The authors included drowsiness in their total sleep time value of 9.2 hr (63.4%) of the recording period. Excluding drowsiness, total sleep comprised 7.8 hr (53.8%) of recording time. Animals were recorded while in restraining collars.

Bert *et al.* [33] recorded sleep EEGs of nine adult bonnet monkeys, *Macaca radiata*, while seated in restraining chairs for a total of 48 nights (10.5-hr–13-hr recordings). Sleep occupied an average of 78.8% (8.27–10.24 hr) of each recording session.

Bert *et al.* [29] have studied the sleep of baboons, *Papio papio*, in the laboratory and under "natural" conditions. In the laboratory, eight adult monkeys were electrographically recorded during the dark period of a 12L/12D photoperiod for a total of 60 nights. During recording sessions animals were seated in restraining chairs. Under these conditions, monkeys slept for an average of 9.4 hr (77.9%).

Eight additional monkeys were electrographically recorded, via telemetry, while housed in "wire-netting cages (3×3×2 m) placed in the forest gallery . . . in the environment in which they had always lived." Monkeys were recorded in pairs during 3 consecutive nights (1900 hr to 0700 hr). Each monkey was also recorded once for a continuous 24-hr period. Under these conditions, monkeys slept 8.8 hr (73.5%) during nocturnal recordings. Seven monkeys showed little sleep during the day, averaging 8.1 min (range=0 to 13.7 min). One monkey slept for 43 min during the day.

The sleep of another species of baboon, *Papio anubis*, was studied by Balzamo and Bert [19]. Four adult females were electrographically recorded over 6 to 8 nights (1800 hr to 0600 hr), while confined in restraining chairs. Sleep duration averaged 9.8 hr, or 82% of the recording period.

Bert [27] also studied six adult female baboons, *Papio hamadryas*, electrographically during nocturnal recording sessions (1800 hr to 0630 hr), while animals were seated in restraining chairs. Sleep comprised 78.7% (9.8 hr) of the recording period.

Finally, the average sleep duration of two adult female baboons, *Papio cynocephalus*, was measured by Balzamo [18]. While animals were in restraining chairs, they were electrographically recorded during the dark portion of a 16.5L/7.5D photoperiod. Sleep comprised 82.5% (6.2 hr) of the recording session.

Three adult chimpanzees, two *Pan troglodytes troglodytes* and one *Pan troglodytes schweinfurthi*, were telemetrically recorded while unrestrained in their home cages, under conditions of natural illumination (a very dim light was used at night for observation) [31]. Based on 14-hr nocturnal recordings (1700 hr to 0700 hr), average sleep duration was reported to be 9.7 hr (69.3%). One animal was observed to nap briefly on two occasions during the day.

Freemon *et al.* [64] telemetrically recorded the EEGs of two unrestrained 4-year-old chimpanzees during 12-hr periods on seven consecutive nights (1900 hr to 0700 hr). Animals slept an average of 10.8 hr (90.1%). In addition, naps were sometimes observed, usually between 1200 hr and 1330 hr.

Riss and Goodall [146] observed the sleep behaviors of six adolescent and young adult chimpanzees housed in a large (30×120 m) outdoor enclosure joined by metal cages. During a 12-day period in which cages were available to the animals, they generally slept inside, retiring between 1748 hr and 1805 hr (sunset was 1940 hr) and arising at sunrise (0610 hr). Total sleep time then was about 12 hr. During 17 days in which monkeys were forced to sleep outside, they retired later (1905 hr to 1920 hr) and awakened slightly later (0640 hr).

Recently, an extensive review article on the ethology and ecology of sleep in monkeys and apes has been published [13]. While sleep duration is not specifically addressed, this paper is noteworthy in that activities associated with the sleep process are described in detail.

With regard to sleep, Primates may be divided into two general groups based on the placement of the major sleep episode. Whereas members of Prosimia generally sleep during the day and their sleep is often polyphasic, the Anthropoidea generally exhibit monophasic nocturnal sleep placement. However, such sleep patterns in the latter group may be a partial function of the typical experimental paradigm in which animals are recorded only during the dark portion of the photoperiod and are virtually always seated in restraining chairs.

Edentates. De Moura Filho *et al.* [47] studied the sleep and waking of 24 three-toed sloths, *Bradypus tridactylus*, by means of behavioral observation and electrographic recording. Normative sleep measures were reported for a subgroup of ten of the animals, observed and recorded during 24-hr periods (EEG recordings of 90 sec out of each 15-min period). Animals were maintained in a modified natural light photoperiod: natural daylight, dim illumination at night to allow observation. Animals were judged to be behaviorally asleep 69.4% (16.7 hr) of the 24-hr day. Electrographic recordings revealed average total sleep time of 66% (15.9 hr per 24 hr). The discrepancy between behavioral and electrographic sleep amounts occurred because the EEG record showed sleep when waking behavior was observed, and conversely behavioral sleep sometimes was accompanied by waking EEG. Morning hours (0600 hr–1200 hr) were comprised primarily of sleep, but sleep also occurred throughout the 24-hr day.

In a field study, Sunquist and Montgomery [179] reported, more generally, total inactivity times of six two-toed sloths, *Choloepus hoffmanni*, to average 16.4 hr per 24 hr (68.3%), and of four three-toed sloths, *Bradypus infuscatus*, to average 13.9 hr per 24 hr (57.9%).

The sleep of three giant South American armadillos, *Prionodontes giganteus*, has been electrographically recorded for three consecutive days [2,3]. Mean total sleep time was 18.1 hr, or 75.4% of the 24-hr day.

A similar total sleep time (18.5 hr per 24 hr) was reported for five nine-banded armadillos, *Dasypus novemcinctus*, electrographically recorded for 24-hr periods. Sleep was polyphasic, with short episodes of wakefulness interrupting sleep throughout the 24 hr. Eleven to 19 sleep periods occurred per 24 hr, ranging in duration from 0.75 to 375 min. Animals often were observed to fall asleep suddenly during eating, "sometimes without finishing the bite of food in their mouth" [139].

Van Twyver and Allison [207] studied thirteen armadillos, *Dasypus novemcinctus*, using continuous 24-hr electrographic recordings. Animals were maintained on a 12L/12D cycle prior to and during the study. Average total sleep time comprised 72.5% (17.4 hr) of the recording period. Waking was found to occur primarily in one major period, lasting 3–5 hr, during the evening. During sleep, the animals could be handled without eliciting arousal responses.

Lagomorphs. Narebski *et al.* [126] electrographically recorded nine rabbits, *Oryctolagus cuniculus*, during at least two 24-hr periods. Mean total sleep time comprised 28.7% (6.9 hr) of the 24-hr day. Two ovariectomized rabbits, recorded continuously for 48 hr under conditions of a 14L/10D illumination schedule, were found to sleep 8.8 hr (37%) of each 24-hr period [172].

Rodents. Rodents are well represented in the literature regarding sleep duration. Observational and/or electrographic studies have been conducted on at least 28 species representing 13 families, to evaluate normative aspects of sleep.

Snyder *et al.* [170] used telemetry to study sleep duration of mountain beavers, *Aplodontia rufa*, over eight 24-hr periods (12L/12D photoperiod). Sleep, including a "transitional state," comprised 60% (14.4 hr) of each 24-hr session. A "pronounced and regular" 5–6 cycles per day sleep-waking rhythm was observed in this species.

The 24-hr sleep durations of three species of ground squirrels have been measured. Van Twyver [202] recorded the EEGs of six thirteen-lined ground squirrels, *Citellus*

tridecemlineatus, continuously for 48 hr. Animals were also observed during the light period of each 12L/12D cycle. Average sleep duration per 24 hr was 13.9 hr, or 58% of the period. Sleep time was relatively evenly distributed across the photoperiod.

Five arctic ground squirrels, *Citellus undulatus parryi*, were observed for an average duration of 210 hr per animal while housed in an outdoor enclosure during continuous arctic daylight [62]. Average sleep time was calculated to be 16.6 hr (69%) during the 24-hr day.

Haskell *et al.* [71] electrographically recorded six golden-mantled ground squirrels, *Citellus lateralis*, for three consecutive 24-hr periods (12L/12D photoperiod). Total sleep time averaged 14.5 hr per 24 hr (60.6%). Two thirds of total sleep occurred during the dark phase.

The sleep patterns of two species of chipmunks have been reported by Estep *et al.* [49]. Twelve eastern chipmunks, *Tamias striatus*, and twelve cliff chipmunks, *Eutamias dorsalis*, were observed continuously during 24-hr periods under a 14L/10Dim photoperiod. Sleep was found to comprise 68% (16.3 hr) of the observation period in *E. dorsalis* and 62% (14.9 hr) of the period in *T. striatus*. In both species sleep occurred predominantly during the dark period. Slight gender differences were noted with males sleeping more in both species.

Five pocket mice, *Perognathus longimembris*, were electrographically recorded for an 8-hr period during the "major nocturnal sleep period" [214]. Sleep comprised 77% to 86% (6.2 hr–6.9 hr) of recording time.

Baumgardner *et al.* [22], in an observational study, evaluated the 24-hr sleep durations of twelve species of the family *Cricetidae*. Twelve animals of each species (with the exception of *Neofiber affeni*, N=9) were maintained on a 16L/8Dim red photoperiod. Observations were conducted every other hour within the 24-hr period. Sleep times ranged from 6.9 hr (29%) per 24 hr in launcha de campo, *Calomys callosus*, to 15.4 hr (64%) per 24 hr in prairie voles, *Microtus ochrogaster* (see table for other values).

Three additional species of the family *Cricetidae* have been examined. Van Twyver [202] recorded the sleep EEGs of six golden hamsters, *Mesocricetus auratus*, continuously for 48 hr. Behavioral observations were also conducted during the light periods of the 12L/12D photoperiod. Sleep comprised 14.4 hr (60.1%) of each 24-hr period. Sleep episodes continued for an average of 11.4 min and were more frequent during the light period. Kilduff and Dube [99] analyzed the sleep EEGs of three cotton rats, *Sigmodon hispidus*, during continuous 24-hr recording in a 12L/12D photoperiod. Sleep comprised an average of 47.1% (11.3 hr) of the 24-hr recording sessions. An average sleep period continued for 14.5 min.

Based on continuous 24-hr electrographic recordings obtained from eight mongolian gerbils, *Merionis unguiculatus*, Kastaniotis and Kaplan [98] reported an average total sleep time of 15.3 hr per 24 hr (63.7%). Animals slept slightly more during the light period of the 12L/12D photoperiod due to a diurnal weighting in active sleep.

Mendelson [121] electrographically studied the sleep of six adult *Octodon degus* for two 8-hr periods each, one beginning with the onset of the light period and one at the onset of the dark period (12L/12D photoperiod). An average of 6.9 hr or 43.2% of the 16-hr recording session was spent sleeping. Sleep was weighted toward a nocturnal placement with 57.8% of total sleep occurring in the dark period.

Van Twyver [202] electrographically recorded the sleep and waking of six laboratory rats, *Rattus norvegicus* (Long

Evans strain), continuously for 48 hr under a 12L/12D photoperiod. Animals were also observed during the light periods. Total sleep time averaged 13.2 hr (55.2%) per 24 hr, with individual sleep epochs continuing for an average of 6.5 min. Although a portion of each hour throughout the recording session was spent in sleep, animals slept more during the light than during the dark phase.

Van Twyver *et al.* [208] studied six Long Evans and five Sprague-Dawley rats behaviorally and electrographically for 24-hr sessions under 12L/12Dim photoperiod. Long Evans averaged 14.4 hr (59.9%) per 24 hr asleep, and Sprague-Dawleys slept an average of 13.6 hr (56.8%) per 24 hr. Sleep was weighted toward a diurnal placement, and sleep episodes continued for an average of 13.3 min for Long Evans and 13.7 min for Sprague-Dawleys.

Mistlberger *et al.* [122] reported similar sleep measures for seven Sprague-Dawley rats electrographically recorded for 24-hr periods in a 12L/12D photoperiod. Total sleep time comprised 57.1% (13.7 hr) of each 24 hr, with sleep episodes continuing for an average of 13.1 min.

Friedmann *et al.* [65] electrographically recorded sixteen Sprague-Dawley rats for 23-hr sessions (1 hr was used for calibration and animal care) under a 12L/12D photoperiod. Sleep comprised 55.8% (12.8 hr) of the recording sessions.

Borbély and Neuhaus [40], employing telemetry, electrographically recorded sixteen Sprague-Dawley rats continuously for 24 hr. Maintained in a 12L/12D photoperiod, animals averaged 10.9 hr (45.4%) of each 24 hr in sleep. Individual sleep episodes continued for 8.4 min, and sleep was weighted toward a diurnal placement, with 75% of the light period and 16% of the dark period spent asleep.

Finally, Kiyono [100] electrographically recorded eighteen rats, Gunn strain, continuously for 24 hr. Total sleep time averaged 54.9% (13.2 hr) of each 24 hr. Animals were maintained on a 12L/12D photoperiod.

Valatx and Bougat [200] electrographically recorded ninety laboratory mice, *Mus musculus*, from six inbred strains. Animals were maintained on a 12L/12D photoperiod and were recorded continuously during 24-hr sessions. Average sleep duration was reported to be 12.8 hr (53.3%) per 24 hr. Slight differences in duration as a function of strain were noted, ranging from 12.1 hr to 13.5 hr per 24 hr.

Several other groups have examined sleep length in laboratory mice. All report sleep durations of between 12 and 14 hr per 24 hr [66, 123, 202]. Baumgardner *et al.* [22] have reported substantially shorter sleep lengths, 8.5 hr per 24 hr (35.4%), using observational data and a 16L/8Dim photoperiod. These authors report the same sleep length for twelve African striped mice, *Rhabdomys prinulus*, observed under the same conditions.

Friedmann *et al.* [66] electrographically recorded eleven wild mice (species unspecified) continuously for 24 hr in a 12L/12D photoperiod. Substantial variability in sleep duration between animals was observed with a range of from 5.8 hr to 14.9 hr per 24 hr.

Four guinea pigs, *Cavia porcellus*, were electrographically recorded during 24 hr in an unspecified photoperiod [89]. Sleep was reported to comprise 12.6 hr (52.5%) of each 24 hr.

Van Twyver [202], using electrographic and observational measures, recorded sleep of six chinchillas, *Chinchilla laniger*. Animals were recorded continuously for 48 hr under conditions of a 12L/12D photoperiod. Total sleep time averaged 12.5 hr (52.2%) of each 24 hr. Sleep episodes lasted for an average of 6.5 min and sleep was weighted toward a diurnal

nal placement.

Cetaceans. Because of the technical difficulties involved in electrographic recording in a water medium, the majority of studies on the sleep of marine mammals have been observational. Since those electrographic studies which have been conducted suggest that cetaceans may obtain sleep while swimming, behavioral observations may underestimate sleep duration.

Pilleri [137] reported on the sleep duration of Indus dolphins, *Platanista indi*, based on the presence or absence of sound emissions made by these blind, river-dwelling animals. Because they live in constantly flowing water, Indus dolphins never stop swimming. Nevertheless, the author reported sleep duration of about 7 hr per 24 hr, with individual sleep episodes lasting on the order of seconds.

Ten captive Dall porpoises, *Phocoenoides dalli*, observed by McCormick [117], were reported to exhibit no "activity resembling sleep behavior. There is neither catnapping nor surface sleep." In contrast, the author observed two porpoises, *Lagenorhynchus obliquidens*, and seven *Tursiops truncatus* and concluded that these species exhibit both forms of sleep. No measures of sleep duration per 24 hr were given.

Flanigan [54] also visually and acoustically observed four bottlenosed porpoises, *Tursiops truncatus*, for 12.5 to 13 hr per night for ten nonconsecutive nights. Two categories of behavior, quiet "hanging" behavior (QHB) and perhaps stereotypic (counterclockwise) circular swimming (SCS) were considered by the author to meet criteria for behavioral sleep. Gender differences were noted in amounts of each of these states: males spent 50.6% (6.5 hr) of observation time in SCS and 1% (≈ 0.13 hr) in QHB. Females spent 33.7% (≈ 4.4 hr) in SCS and 22.7% (2.9 hr) in QHB. It was suggested that the gender difference may reflect male nocturnal vigilance or differences in age or degree of adaptation.

The sleep EEGs of nine freely swimming bottlenosed dolphins, *Tursiops truncatus*, were recorded by Mukhametov *et al.* [125]. Continuous recordings for up to 72 hr revealed two types of sleep: bilateral synchronization, in which slow waves were recorded from both brain hemispheres, and unilateral synchronization, in which only one hemisphere showed slow wave activity. The sleep percentages given were from one representative animal: bilateral synchronization occupied 0.8% and unilateral occupied 42.4% of recording time (TST=10.4 hr per 24 hr).

Kovalzon [104] electrographically recorded four bottlenosed dolphins continuously for 3–4 days. Unilateral synchronization was observed both while animals were "suspended floating almost immobile" and while they were "slowly swimming around in a counterclockwise direction." Bilateral synchronization was seldom observed. Daily amounts of sleep fluctuated between 0 and 4 hr.

The sleep behavior of two Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, was observed in constant illumination for 12–13 hr per night for 12 consecutive nights [57]. Stereotypic circular (counterclockwise) swimming (SCS) was accompanied by intermittent sleep, and comprised an average of 17.5% of recording time. Quiet hanging behavior (QHB) occupied 10.8% of recording time in one animal, and 2.9% in the other. The majority of QHB occurred during the first and last quarters of the night.

Flanigan [55,58] has also studied the sleep behavior of two species of whales. Two pairs of Beluga whales, *Delphinapterus leucas*, were studied. One pair (both females) studied for 13.5 to 14 hr per night for seven nonconsecutive

nights under constant illumination exhibited stereotypic circular (clockwise) swimming (SCS) which comprised 37.4% of recording time (5.2 hr). Average epoch duration was 7 min. Two animals studied for 12 hr per night for nine consecutive nights under constant illumination (at a different location than the first pair) showed stereotypic in-place "swimming" (SIS) which accounted for 18.1% of observation time in the male and 27.6% in the female. Differences in behaviors between pairs were attributed to pool dissimilarities, adaptation time, age, group make-up or even degree of obesity.

Two killer whales, *Orcinus orca*, were studied for 12–13 hr for 12 consecutive nights also under constant illumination. Quiescent "hanging" behavior (QHB) averaged 10.5% of recording time, with an average epoch length of 9.6 min. QHB was primarily limited to dawn and dusk placement; SCS was not seen in this species.

Shurley *et al.* [167] observed the behavior of a 4-year-old North Pacific pilot whale, *Globicephala scammoni*, and found behavioral sleep to average 22% (5.3 hr) of the 24-hr day. Activity, inactive alert and behavioral sleep were "distributed precisely parallel with gross human activity in the vicinity."

The same animal was subsequently electrographically recorded for three nonconsecutive nights (6–8 hr) over a 7-day period [164]. During recordings the animal was confined in a narrow, shallow channel of the aquarium. Because the whale did not sleep either by behavioral or EEG criteria on the first two nights, she was kept in a state of "prolonged, continuous exertion" throughout the day preceding the third recording night. As a result, the whale slept on this night, but no sleep duration measures were reported.

Carnivores. Wauquier *et al.* [216] analyzed the electrographic records of seven beagle dogs obtained during continuous 24-hr periods under constant illumination. Dogs averaged 53.8% (12.9 hr) of each 24 hr in sleep.

Takahashi *et al.* [182] electrographically recorded ten adult dogs (seven mongrels, three beagles) for 24-hr periods under a 12L/12D photoperiod. Sleep comprised 11.1 hr (46.3%) of the recording period.

Copley *et al.* [43] reported substantially shorter sleep durations in five dogs of unspecified species, studied electrographically and behaviorally over a 48-hr period. Using a 16L/8D photoperiod, these authors found sleep to occupy 31.9% of the recording period (7.7 hr per 24 hr). Sleep was weighted toward a dark-period placement.

Lucas *et al.* [114] also found relatively short sleep durations in six pointer dogs electrographically recorded continuously for 24 hr. The dogs were maintained on a 12L/12D photoperiod, and were not isolated from the 25 other dogs in the colony during recording. Sleep comprised an average of 35% (8.4 hr) of the recording period. The major portion of sleep occurred between 2100 hr and 0400 hr, which was within the dark period of the photoperiod. The average sleep episode continued for 45 min.

In addition to domestic dogs, three other species of Canid have been examined relative to sleep duration. Based on rest/activity measures derived from telemetered heart rate data obtained during continuous Arctic daylight, Folk [61] reported that one Arctic wolf, *Canis lupus*, slept about 13 hr per 24 hr, and that one Arctic fox, *Alopex lagopus*, slept about 12.5 hr per 24 hr. In both animals, sleep was weighted toward a diurnal placement, even during periods of constant light.

Dallaire and Ruckebusch [46] electrographically recorded

three Red foxes, *Vulpes vulpes*, continuously for one week. Sleep comprised 41% (9.8 hr) of each 24-hr period. Sleep episodes averaged 48.5 min (range, 14–106 min), and occurred primarily during the daytime. The major sleep period was between 1600 hr and 2000 hr.

Sterman *et al.* [175] electrographically recorded eight cats, *Felis domestica*, in constant dim red illumination for at least one 24-hr period. Behavioral observations were also carried out during the recording period. Because the first hour of recording was frequently disturbed by food and water replenishment, analyses were based on 23-hr data. Electrographic sleep occupied 57% (13.3 hr) of the 23-hr period (13.8 hr per 24 hr, extrapolated). Behavioral observation revealed a sleep time of 12.7 hr per 23 hr. The period of peak occurrence of sleep was between 1200 hr and 1800 hr.

Ursin [197] electrographically recorded twelve adult cats for two 12-hr sessions under conditions of constant light. Each 24-hr session was interrupted for 2 hr (from 1400 hr to 1600 hr), and for purposes of analyses this interval was included in waking time. Average sleep time per 24 hr was 13.2 hr (55.1%).

In a later study, the same author [198] electrographically recorded three cats continuously for at least 24 hr. Total sleep comprised only 40.5% (9.7 hr) of each 24 hr.

Ruckebusch and Gaujoux [159] studied three adult cats, electrographically and behaviorally, during three periods of five consecutive days. EEGs were recorded continuously during this time while animals were maintained on a 12L/12D photoperiod. During recordings, animals were housed in the same room with 200 rats and 30 rabbits. Time spent asleep averaged 11.3 hr per 24 hr (47.1%). Recorded in continuous light for two periods of five days each, the same animals slept for an average of 9.2 hr per 24 hr (38.1%).

Lucas and Sterman [115] electrographically recorded 18 cats for at least two 24-hr sessions in constant illumination. Mean 24-hr sleep duration was 13.2 hr (54.8%). The mean sleep episode continued for 78 ± 14 min.

Only one additional member of the Felidae family has been examined. Zepelin [223] observed two jaguars, *Panthera onca*, continuously for 48 hr under conditions of constant illumination (natural daylight, artificial illumination at night). Animals were observed in their home pens in a zoological garden. Total sleep time averaged 10 hr per 24 hr, with sleep occurring primarily at night. Sleep epochs generally continued for 50–113 min.

Finally, sleep durations of two species of marine carnivores have been reported. Ridgeway *et al.* [145] electrographically examined four gray seals, *Halichoerus grypus*, using telemetric recordings for twelve 14-hr periods (1800 hr to 0800 hr). Animals were recorded in either a community tank (one session) or in individual tanks (eleven sessions), all under continuous illumination. Sleep comprised an average 6.2 hr of each recording session (44.3%).

Mukhametov [124] electrographically studied an unspecified number of Caspian seals, *Gallerinus ursinus*, under conditions of natural light and darkness. Sleep was found to occupy only 15% (3.6 hr) of the 24-hr recording sessions.

Proboscidea. Sleep durations of two species of elephant, the Asian, *Elephas maximus*, and the African, *Loxodonta africana*, have been reported by Kurt [106]. The animals, thirteen specimens of each species, were observed in stables during 8-hr sessions (2300 hr–0700 hr). Total sleep time was reported to be 3.8 hr in the Asian and 3.3 hr in the African elephants.

Hyracoidea. Snyder [169] telemetrically recorded the

EEGs of three species of this order. Continuous 24-hr recordings were obtained from four rock hyrax, *Heterohyrax brucei*, four rock hyrax, *Procavia johnstoni*, and one tree hyrax, *Dendrohyrax validus*, under conditions of natural light and darkness. Total sleep times comprised 23.7% (5.7 hr), 20.4% (4.9 hr) and 20.4% (4.9 hr) of each 24 hr, respectively. Sleep was distributed relatively evenly across the 24 hr in rock hyrax, and was weighted toward a diurnal placement in the tree hyrax.

Perissodactyla. The sleep durations of three species of odd-toed ungulates have been reported. Ruckebusch ([153]; see also [151]) electrographically recorded three horses, *Equus caballus*, for two to three consecutive 24-hr periods per week, over a period of several months. Animals were housed in barn stalls, under an unspecified photoperiod. Average total sleep time was 2.9 hr (12%) per 24 hr. All sleep occurred during the night, and 80% of sleep occurred while horses remained standing.

Three donkeys, *Equus asinus*, recorded under the same conditions [150], were reported to sleep an average of 3.1 hr (13%) per 24 hr.

Zepelin [223] observed two tapirs, *Tapirus terrestris*, continuously for 48 hr. Animals were housed in a zoo, and cages were illuminated at night. Because sleep criteria may have been somewhat unreliable for tapirs, the author based sleep duration measures on the 24-hr period which was scored most confidently. Total sleep time averaged 4 hr per 24 hr, with individual sleep epochs typically continuing for a maximum of 10 min.

Artiodactyla. Ruckebusch [152] electrographically recorded three specimens each of cows, *Bos taurus*, sheep, *Ovis aries*, and pigs, *Sus domesticus* (see also [161]). Cows were housed in barn stalls, sheep and pigs were recorded in metabolic cages. Under an unspecified photoperiod, animals were recorded for two to three consecutive 24-hr periods per week for several months. Cows slept for an average of 4 hr (17%) per 24 hr, 95% occurring at night. In a later study [157], it was reported that total sleep time was reduced by almost half when cows were recorded in the pasture. Pigs slept for an average of 7.8 hr (33%) per 24 hr, two thirds of which occurred at night. Total sleep time for sheep averaged 3.8 hr (16%) per 24 hr, 87% of which occurred at night.

Ladewig and Ellendorf [107] studied the sleep of three German Landrace pigs electrographically and via time-lapse video recording. Following at least two weeks of adaptation to the recording situation each animal was recorded for ten 24 hr periods within 20 days. Photoperiod was not specified. Average sleep duration comprised 43.4% (10.3 hr) of each 24 hr period.

Bell and Itabisashi [23] electrographically recorded ten Saanen goats, *Capra aegagrus hircus*, under constant dim illumination for two 13.5-hr sessions (1700 hr–0630 hr). Sleep was found to comprise an average of 39.8% (5.37 hr) of the recording session.

Two species of wild artiodactyla have been studied. Immelmann and Gebbing [86] observed three giraffes, *Giraffa camelopardalis reticulata*, and one okapi, *Okapia johnstoni*, during 14 nights in a zoological garden. It is not clear from the study whether sleep durations reported were for total sleep time or for portions of sleep (e.g., paradoxical sleep, slow wave sleep). Nevertheless, values for the giraffes averaged 20 min per night with the longest episode continuing for 12 min. Measures for the okapi averaged 60 min per night with a period length of 5–6 min.

Finally, in addition to the studies cited above a book by

Hassenberg [72] should be mentioned. It describes in detail (with numerous illustrations) sleep postures and preparatory behavior in a large number of mammalian species.

THE TABLE

The following table is a comprehensive listing of representative sleep values for each species for which sleep (or rest) duration measures have been reported in the literature. The table does not include all species discussed in the previous section, because definite sleep (rest) duration measures were not provided by the authors (e.g., in tree frogs). When more than one study was available for a species, representative studies presented in the table were selected with regard to the following criteria: (1) length of recording time; studies employing at least 24-hr recordings were selected when available, (2) specification of the photoperiod employed; studies employing the natural light-dark cycle were preferred, followed by 12L/12D, 12L/12Dim, other L/D schedules, L/L or D/D schedules, (3) specification of sleep period length, (4) number of animals studied. In the few instances in which more than one study met these criteria to an equal degree, the study appearing in the table

was selected arbitrarily. In addition, in the interest of providing a complete survey, some references given in the table were chosen, often in spite of limitations, because they were the only studies available. Many of these are in abstract form, and are noted in the table. Total sleep or rest times presented should not necessarily imply continuous 24-hr recordings or observations.

Other-than-24-hr recording sessions have been noted in parentheses under the sleep duration values. Drowsiness or transitional states are not included in total sleep times except where authors did not discriminate between sleep and these states. These instances are noted.

Often animals do not obtain 24-hr sleep quotas during a single sleep period, but rather exhibit polyphasic sleep patterns. When specifically stated by the authors, sleep episode duration and the placement of sleep within the nycthemeron is noted in the table.

The order in which species are presented in the table follows the traditional systematic classification of animals [189]. Such a taxonomy is based primarily on the similarity of structural features, i.e., skeletal, dental rather than, for example, degree of brain development or behavioral similarity.

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
Invertebrates									
cockroach <i>Leucophea maderae</i>	26	12L/12Dim	14 hr		+	++++	*		[191]
Fish									
perch <i>Perca fluviatilis</i>	10	natural	5-10 hr			++++	*		[168]
red-eye <i>Scardinius erythrophthalmus L.</i>		natural	1-3 hr			++++	*		[168]
guppy <i>Tilapia mossambica</i>	30	15L/9Dim	6.5-7.5 hr		+	+++	*		[165]
tench <i>Tinca tinca L.</i>	25	12L/12D	14.4 hr	15-20 min	+	+++		*	[134]
Amphibians									
bullfrog <i>Rana catesbiana</i>	10	natural	0 hr				*	*	[78]
lake frog <i>Rana ridibunda</i>	6		2.4 hr				*	*	[]
western toad <i>Bufo boreas</i>		natural	14.6 hr	25 ± 15 min	+	+++	*	*	[83]
smooth newt <i>Triturus vulgaris</i>	20	stimulated	4.6 hr (water)						
		natural	11.0 hr (land)			++++	*		[76]
Reptiles									
North American box turtle <i>Terrapene carolina</i>	11	constant illumination	19-21.8 hr					*	[59]

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
red-footed tortoise		constant	11-11.7 hr						
<i>Geochelone carbonaria</i>	6	illumination	(12-13 hr record)				*		[54]
European pond turtle									
<i>Emys orbicularis</i>			6.9 hr						[95]
marginated tortoise								*	
<i>Testudo marginata</i>			11.5 hr						[75]
Sea turtle		constant							
<i>Caretta caretta L.</i>	3	illumination	0 hr				*	*	[180]
tortoise									
<i>Testudo denticulata</i>	7	12L/12D	0 hr				*	*	[213]
caiman									
<i>Caiman sclerops</i>	5	12L/12D	3.0 hr	16 min	+++	+	*	*	[120]
caiman									
<i>Caiman latirostris</i>	1		12.5 hr					*	[135]
alligator									
<i>Alligator mississippiensis</i>	7		0 hr				*	*	[203]
black iguana									
<i>Ctenosaura pectinata</i>	23	12L/12D	6-9 hr (12 hr record)		++++		*		[184]
green iguana			4.2-7.9 hr						
<i>Iguana iguana</i>	3	12L/12Dim	(12 hr record)		++++		*	*	[53]
desert iguana									
<i>Dipsosaurus dorsalis</i>	8	12L/12D	16.3-17.8 hr					*	[84]
horned lizard									
<i>Phrynosoma regali</i>	13	12L/12D	12.3 hr		++++		*	*	[149]
African python									
<i>Python sebae</i>	1		15.6-20.4 hr					*	[134]
Birds									
white leghorn chicken									
<i>Gallus domesticus</i>	17		11.7 hr					*	[95]
landaise goose									
<i>Anser anser</i>	4	12L/12D	6.2 hr		++	++		*	[48]
domestic duck									
<i>Anas platyrhynchos</i>	4	11L/11D/ 2Dim	10.8 hr		++	++	*	*	[225] A
hawk									
<i>Buteo jamaicensis</i>	1		4-5 hr	3-40 min	++++		*	*	[148]
arboreal falcon									
<i>Herpetotheres cachinnans</i>	1		4-5 hr	3-40 min	++++		*	*	[148]
emperor penguin									
<i>Aptenodytes forsteri</i>	4	natural	10.7 hr	4.7-5 min	++	++		*	[48]
little penguin									
<i>Eudyptula minor</i>	5	12L/12Dim	8.3 hr		+++	+		*	[173]
domestic pigeon									
<i>Columba livia</i>	8	12L/12Dim	10.6 hr	7.0 min	+++	+	*	*	[207]
ring-necked dove									
<i>Streptopelia capicola</i>		12L/12D	10.2 hr		++++			*	[214] A
parakeet		constant illumination	9.4 hr					*	[209]
<i>Aratinga canicularis</i>									
burrowing owl									
<i>Speotyto cunicularis</i>	4	12L/12D	14.3 hr		++	++	*	*	[25]
<i>hypugaea</i>	2	12L/12D	16.0 hr		++	++	*	*	[181]
<i>Strix aluco</i>									

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
polar white owl <i>Nyctea scandiaca</i>			7.9 hr					*	[95]
starling <i>Sturnus vulgaris</i>	6	natural/ 12L/12D	4.7-4.9 hr (12 hr record)		++++			*	[195]
chaffinch <i>Fringilla coelebs</i>	5	natural/ 12L/12D	7.0 hr (12 hr record)		++++			*	[196]
Sleep duration of 31 species of wild birds based on behavioral data as compiled by Amlaner and Ball (1983) follows:									
hoary redpoll <i>Acanthis hornemanni</i>		constant illumination	3.4 hr		++++			*	
pintail <i>Anas acuta</i>		10.4L/13.6D	8.1 hr			++++		*	
green-winged teal <i>Anas crecca carolinensis</i>		10.4L/13.6D	8.0 hr			++++		*	
green-winged teal <i>Anas crecca crecca</i>		8.9L/15.1D	8.2 hr			++++		*	
black duck <i>Anas rubripes</i>		15.6L/8.4D	6.9 hr		++	++		*	
common swift <i>Apus apus</i>		13.5L/10.5D	10.6 hr		++++			*	
European pochard <i>Aythya ferina</i>		15.5L/8.5D	12.8 hr		++	++		*	
tufted duck <i>Aythya fuligula</i>		13.7L/10.3D	13.2 hr		++++			*	
European golden-eye <i>Bucephala clangula</i>		10.8L/13.2D	6.4 hr		++++			*	
purple sandpiper <i>Calidris m. maritima</i>		constant illumination	3.5 hr			++++		*	
semipalmated sandpiper <i>Calidris pusilla</i>		constant illumination	2.7 hr		++++			*	
Anna's hummingbird <i>Calypte anna</i>		11L/13D	11.1 hr		++++			*	
grey-cheeked thrush <i>Catharus minimus</i>		constant illumination	3.3 hr		++++			*	
trumpeter swan <i>Cygnus c. buccinator</i>		14.9L/9.1D	5.7 hr		+++	+		*	
whooper swan <i>Cygnus c. cygnus</i>		18.3L/5.7D	12.0 hr		+	+++		*	
house martin <i>Delichon urbica</i>		constant illumination	3.3 hr		++++			*	
herring gull <i>Larus argentatus</i>		15.9L/8.1D	5.0 hr		+++	+		*	
wild turkey <i>Meleagris gallapavo</i>		11.8L/12.2D	3.9 hr		++++			*	
smew <i>Mergus albellus</i>		11.7L/12.3D	13.4 hr		++++			*	
wheatear <i>Oenanthe oenanthe</i>		constant illumination	4.8 hr		++++			*	
great tit <i>Parus m. major</i>		15.6L/8.4D	8.0 hr		++++			*	
chestnut-backed chickadee <i>Parus rufescens</i>		11.8L/12.2D	11.7 hr		++++			*	

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference	
					Dark Night	Light Day	B	E		
red phalarope										
<i>Phalaropus fulicarius</i>		constant illumination	3.1 hr			++++		*		
snow bunting		constant illumination	4.6 hr			++++		*		
<i>Plectrophenax nivalis</i>		constant illumination	6.3 hr			++++		*		
kittiwake		constant illumination	4.3 hr				++++	*		
<i>Rissa tridactyla</i>		constant illumination	12.8 hr			++++		*		
Arctic tern		constant illumination	3.5 hr				++++	*		
<i>Sterna paradisaea</i>		constant illumination	3.9 hr				++++	*		
barred owl		14.1L/9.9D	11.3 hr			++++		*		
<i>Strix varia</i>		constant illumination	3.7 hr			++++		*		
Bewick wren		11.9L/12.1D								
<i>Thryomanes bewickii</i>		constant illumination								
American robin		constant illumination								
<i>Turdus migratorius</i>		constant illumination								
Mammals										
Montremes										
echidna										
<i>Tachyglossus aculeatus</i>	5		8.6 hr	27 min		+	+++	*	*	[9]
Marsupials										
North American opossum										
<i>Didelphis marsupialis</i>	5	constant illumination	19.4 hr	1-4 hr		+	+++	*	*	[205]
little water opossum										
<i>Lutreolina crassicaudata</i>	20		19.4 hr						*	[2]
phalanger										
<i>Trichosurus vulpecula</i>	3		13.7 hr						*	[112]
Red kangaroo			0.78-2.1 hr							
<i>Megaleia rufa</i>	5	natural	(5.5 hr record)					*		[42]
kangaroo rat										
<i>Potorous apicalis</i>	4	12L/12D	11.6 hr			+	+++		*	[17]
Insectivores										
European hedgehog										
<i>Erinaceus europaeus</i>	9		10.1 hr	17 ± 3.7 min		+	+++		*	[193]
Desert hedgehog										
<i>Paraechinus hypomelas</i>			10.3 hr			+	+++		*	[184] A
Eastern mole										
<i>Scalopus aquaticus</i>	6	constant illumination	8.4 hr	1-3 hr						
star-nosed mole		constant illumination								
<i>Condylura cristata</i>	1	illumination	10.3 hr	1-3 hr				*	*	[8]
European mole										
<i>Talpa europaea</i>	8	natural	10.5 hr	2.2-4.7 hr				*		[67]
tree shrew										
<i>Tupaia glis</i>	6	12L/12D	8.9 hr			+++	+	*	*	[26]
lesser short-tailed shrew		constant illumination or								
<i>Cryptotis parva</i>	3	12W/12R	9.1 hr			+	+++	*		[6]
greater short-tailed shrew		constant illumination								
<i>Blarina brevicauda</i>	1	illumination	14.9 hr					*		[6]

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
musk shrew <i>Suncus murinus</i>	7	constant low-level illumination	12.8 hr		++	++	*	*	[6]
common shrew <i>Sorex araneus</i>	4	12L/12D	7.8 hr	12-36 min	+	+++			[44]
pygmy shrew <i>Sorex minutus</i>	2	12L/12D	8.5 hr		+	+++			[44]
water shrew <i>Neomys fodiens</i>	1	12L/12D	13.6 hr		++	++		*	[44]
tenrec <i>Centetes ecaudatus</i>		12L/12D	15.6 hr (drowsiness included)					*	[170] A
<i>Chiroptera</i>									
little brown bat <i>Myotis lucifugus</i>			19.9 hr					*	[41] A
big brown bat <i>Eptesicus fuscus</i>			19.5 hr						[224]
<i>Primates</i>									
slow loris <i>Nycticebus coucang</i>	6	natural and dim red	11.0 hr				++++	*	[188]
bushbaby <i>Galago senegalensis</i>	15		7.8 hr (8 hr record)				++++		[30]
lemur <i>Lemur macaco fulvus</i>	1		9.4 hr	3.3 hr				*	[211]
lemur <i>Phaner furcifer</i>		natural	11-12 hr				++++	*	[130]
owl monkey <i>Aotus trivirgatus</i>	3	12L/12D	17 hr		+	+++		*	[133]
squirrel monkey <i>Saimiri sciureus</i>	3	12L/12D	9.9 hr (12 hr record)				++++		[1]
vervet <i>Cercopithecus aethiops</i>	4	12L/12D	10.3 hr (13.5 hr record)				++++		[32]
sabaeus <i>Erythrocebus patas</i>	4	12L/12D	10.8 hr (13.5 hr record)				++++		[32]
patas monkey <i>Macaca mulatta</i>	34	12L/12D	11.8 hr		+++	+		*	[45]
pigtail macaque monkey <i>Macaca nemestrina</i>	6		7.8 hr (14.5 hr record)				++++	*	[143]
bonnet monkey <i>Macaca radiata</i>	9	12L/12D	8.3-10.2 hr (10.5-13 hr record)				++++		[33]
baboon <i>Papio papio</i>	8	12L/12D	9.4 hr (12 hr record)				++++		[29]
baboon <i>Papio papio</i>	8	natural	8.8 hr (field)				++++	*	[29]
baboon <i>Papio anubis</i>	4		9.8 hr (12 hr record)				++++		[19] A
baboon <i>Papio hamadryas</i>	6		9.8 hr (12.5 hr record)				++++		[27]
baboon <i>Papio cynocephalus</i>	2	16.5L/7.5D	6.2 hr (7.5 hr record)				++++		[18]
chimpanzee <i>Pan troglodytes</i>	3	natural + dim nocturnal	9.7 hr (14 hr record)				++++	*	[31]
<i>Edentates</i>									
three-toed sloth <i>Bradypus infuscatus</i>	10	natural + dim at night	15.8 hr		++	++		*	[47]
two-toed sloth <i>Choloepus hoffmanni</i>	6	natural	16.4 hr					*	[179]

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
Giant armadillo <i>Priodontes giganteus</i>	3		18.1 hr					*	[2]
Nine-banded armadillo <i>Dasyus novemcinctus</i>	13	12L/12D	17.4 hr			++	++		[207]
Lagomorphs rabbit <i>Oryctolagus cuniculus</i>	2	14L/10D	8.8 hr					*	[172]
Rodents mountain beaver <i>Aplodontia rufa</i>		12L/12D	14.4 hr (drowsiness inclusive)						[170] A
thirteen-lined ground squirrel <i>Citellus tridecemlineatus</i>	6	12L/12D	13.9 hr			++	++	*	[204]
Arctic ground squirrel <i>Citellus undulatus parryi</i>	5	continuous natural light	16.6 hr (field)					*	[62]
golden-mantled ground squirrel <i>Citellus lateralis</i>	6	12L/12D	14.5 hr			+++	+	*	[71]
Eastern chipmunk <i>Tamias striatus</i>	12	14L/10Dimred	16.3 hr			+++	+	*	[49]
cliff chipmunk <i>Eutamias dorsalis</i>	12	14L/10Dimred	14.9 hr			+++	+	*	[49]
pocket mouse <i>Perognathus longimembris</i>	5		6.2-6.9 hr (8 hr record)			++++		*	[214] A
cactus mouse <i>Peromyscus erimicus</i>	12	16L/8Dim	10.9 hr				++++	*	[22]
cotton mouse <i>P. gossypinus</i>	12	16L/8Dim	7.8 hr				++++	*	[22]
white-footed mouse <i>P. leucopus</i>	12	16L/8Dim	7.8 hr				++++	*	[22]
deer mouse <i>P. maniculatus bairdi</i>	12	16L/8Dim	12.9 hr				++++	*	[22]
old field mouse <i>P. polionotus</i>	12	16L/8Dim	13.1 hr				++++	*	[22]
Northern grasshopper mouse <i>Onychomys leucogaster</i>	12	16L/8Dim	14.5 hr				++++	*	[22]
gray-tailed vole <i>Microtus canicaudus</i>	12	16L/8Dim	10.8 hr			++	++	*	[22]
mountain vole <i>M. montanus</i>	12	16L/8 Dim	11.4 hr			++	++	*	[22]
prairie vole <i>Microtus ochrogaster</i>	12	16L/8Dim	15.9 hr			++	++	*	[22]
meadow vole <i>M. pennsylvanicus</i>	12	16L/8Dim	13.7 hr			++	++	*	[22]
launcha de campo <i>Calomys callosus</i>	12	16L/8Dim	7.0 hr				++++	*	[22]
round-tailed muskrat <i>Neofiber affeni</i>	9	16L/8Dim	14.6 hr			++	++	*	[22]

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
golden hamster									
<i>Mesocricetus auratus</i>	6	12L/12D	14.4 hr	11.4 min	+	+++	*	*	[202]
cotton rat									
<i>Sigmodon hispidus</i>	3	12L/12D	11.3 hr	14.5 min				*	[99] A
Mongolian gerbil									
<i>Merionis unguiculatus</i>	8	12L/12D	15.3 hr		++	++		*	[98] A
laboratory rat (Long Evans)									
<i>Rattus norvegicus</i>	6	12L/12D	13.2 hr	6.5 min	+	+++	*	*	[202]
laboratory rat (Sprague-Dawley)									
<i>Rattus norvegicus</i>	7	12L/12D	13.7 hr	13.1 min	+	+++		*	[122]
laboratory rat (Gunn)									
<i>Rattus norvegicus</i>	18	12L/12D	13.2 hr					*	[100] A
African striped mouse									
<i>Rhabdomys prinulus</i>	12	16L/8Dim	8.5 hr					*	[22]
laboratory mouse									
<i>Mus musculus</i>	90	12L/12D	12.8 hr					*	[200]
guinea pig									
<i>Cavia porcellus</i>	4		12.6 hr					*	[89]
chinchilla									
<i>Chinchilla laniger</i>	6	12L/12D	12.5 hr	6.5 min	+	+++	*	*	[202]
degu			6.9 hr						
<i>Octodon degu</i>	6	12L/12D	(16 hr record)		+++	+		*	[121] A
Cetaceans									
Indus dolphin									
<i>Platanista indi</i>			7.0 hr	seconds				*	[137]
Dall porpoise									
<i>Phocoenoides dalli</i>	10		0 hr					*	[117]
bottlenosed dolphin									
<i>Tursiops truncatus</i>	9		10.4 hr					*	[125]
Pacific white-sided dolphin									
<i>Lagenorhynchus obliquidens</i>	2	continuous illumination	0.4-1.3 hr (12-13 hr record)					*	[57] A
Beluga whale			5.2 hr						
<i>Delphinapterus leucas</i>	2	constant illumination	(13.5-14 hr record)	7 min	++++			*	[55] A
killer whale			1.3 hr						
<i>Orcinus orca</i>	2	illumination	(12-13 hr record)	9.6 min	++++			*	[58] A
North Pacific pilot whale									
<i>Globicephala scammoni</i>	1		5.3 hr		+++	+		*	[167]
Carnivores									
domestic dog (beagle)									
<i>Canis domesticus</i>	7	constant illumination	12.9 hr	45 min	+++	+		*	[216]
domestic dog (pointer)									
<i>Canis domesticus</i>	6	12L/12D	8.4 hr		+	+++			[114]
Arctic wolf									
<i>Canis lupus</i>	3	natural constant light	13.0 hr		+	+++			[61]
Arctic fox									
<i>Alopex lagopus</i>	7	natural constant light	12.5 hr	48.5 min	+	+++		*	[61]
Red fox									
<i>Vulpes vulpes</i>	3		9.8 hr	78 ± 14 min	+	+++		*	[46]
domestic cat									
<i>Felis domestica</i>	18	constant illumination	13.2 hr	50-113 min	+++	+		*	[115]

(Continued)

TABLE 1
SLEEP DURATIONS FOR 168 SPECIES
(Continued)

Class/Species	N	Photo-period	Total Sleep (Rest) Time/24 hr	Sleep (Rest) Episode Length	Sleep (Rest) Placement		Measurement		Reference
					Dark Night	Light Day	B	E	
jaguar <i>Panthera onca</i>	2	illumination	10.0 hr				*		[223] A
gray seal <i>Halichoerus grypus</i>	4	illumination	(14 hr record)		+++		*	*	[145]
Caspian seal <i>Gallerinus ursinus</i>		natural	3.6 hr					*	[124]
Proboscidea									
Asian elephant <i>Elephas maximus</i>	13	natural	3.8 hr (8 hr record)		++++		*		[106]
African elephant <i>Loxodonta africana</i>	13	natural	3.3 hr (8 hr record)		++++		*		[106]
Hyracoidea									
rock hyrax <i>Procavia johnstoni</i>	4	natural	4.9 hr		++	++		*	[169] A
rock hyrax <i>Heterohyrax brucei</i>	4	natural	5.7 hr		++	++		*	[169] A
tree hyrax <i>Dendrohyrax validus</i>	1	natural	4.9 hr		+	+++		*	[169] A
Perissodactyla									
horse <i>Equus caballus</i>	3		2.9 hr		++++			*	[153]
donkey <i>Equus asinus</i>	3		3.1 hr		++++			*	[153]
tapir <i>Tapirus terrestris</i>	2	natural + dim at night	4.4 hr	<10 min				*	[223] A
Artiodactyla									
sheep <i>Ovis aries</i>	3		3.8 hr		+++	+		*	[152]
cow <i>Bos taurus</i>	3		4.0 hr		+++	+		*	[153]
pig <i>Sus domesticus</i>	3		7.8 hr		+++	+		*	[161]
goat <i>Capra aegagrus hircus</i>	10	constant illumination	5.37 hr (13.5 hr record)		++++			*	[23]

Studies from which values were taken are shown at right; an "A" following the citation indicates data presented in an abstract only. Under heading "Measurement", "B" signifies behavioral observation, "E" signifies electrographic recordings were made. If recordings were carried out for less than 24 hours, recording time appears in parentheses under Total Sleep (Rest) Time/24 hr. N=number of animals used in citation.

DISCUSSION

Methodological Issues

In the previous section we have surveyed the literature regarding sleep or rest characteristics of 170 animal species. The reports presented here, to our knowledge, comprise the entire data base concerning sleep duration in animals. In reviewing the literature it became apparent that certain methodological problems put severe constraints on the ability to compare sleep duration measures across orders and species, and in some cases, to compare sleep lengths reported from different laboratories for the same species.

Clearly a major difficulty is the definition of sleep itself, and this problem was discussed in the last section. In addition, however, numerous experimental conditions may also contribute to the difficulty in obtaining reliable and valid measures of sleep duration and placement.

Probably the most important single factor in the study of animals under laboratory conditions is *adaptation* to that environment. There is general agreement that the sleep durations recorded from a well-adapted animal, under laboratory conditions, reflect the animal's maximal capacity for sleep (excluding sleep following manipulations such as sleep deprivation or drug treatment), rather than its typical sleep length under natural conditions.

If all species became adapted to such conditions at the same rate and to the same degree sleep duration measures, whether reflecting maximal capacity for sleep or not, would provide a normative data base amenable to comparison. However, it is clear that different species require differing amounts of time in order to adapt to the laboratory environment, and some species probably never adapt to the degree that others do. Allison and Van Twyver [7] reported that adaptation times in mammalian species ranged from a few

hours (e.g., moles) to a few months (e.g., horses). These authors were able to classify species as "good" or "poor" sleepers on the basis of time required for adaptation to the laboratory environment.

That adaptation time may be highly species-specific is suggested by the finding that rodents required from several days (chinchillas) to several weeks (squirrels) between being placed into recording chambers and exhibiting normal sleep behaviors and electrographic patterns [202]. Well-adapted guinea pigs have been shown to sleep twice as much as guinea pigs not sufficiently adapted to the same conditions [89].

Even strain differences may result in different adaptation times. Laboratory mice recorded continuously for 20 days immediately following electrode implantation slept 3.5 hr longer on days one through three post surgery as compared to days 12 through 20. Stabilization of sleep patterns and durations were strain-specific and ranged from six to 12 days [199,200].

Domestic herbivores are highly sensitive to housing conditions and are easily disturbed. As mentioned above, horses require up to three months habituation to the recording situation to exhibit all behavioral signs of sleep. Even after initial adaptation, one awakening elicited by a startling stimulus typically causes these animals to remain vigilant for the rest of the night [151,156]. Cows have been shown to sleep almost twice as long in their home stalls as in a paddock with which they were also familiar [154, 155, 157]. Indeed, the problem of adaptation appears to be ubiquitous, ranging from amphibians (e.g., [78]) to primates (e.g., [28,29]).

The degree to which the effects of adaptation to the laboratory may influence sleep duration measures may be largely attenuated by allowing sufficient time for habituation. To make certain that sufficient time has been allowed, it is desirable that recordings be made until consistent measures are obtained across several successive recording sessions. This may be particularly critical following surgical interventions. Such stabilization would clearly enhance the reliability of sleep length measures.

A primary variable in the speed and degree with which animals become adapted to the laboratory environment is the extent to which such environments resemble the animal's natural habitat. Factors such as photoperiod, light intensity, ambient temperature, nutritional requirements, and seasonal variation all have potential effects on sleep length measures.

The importance of *light-dark schedules* as *Zeitgebers* for virtually every biological rhythm thus far examined is well known. That rhythms become entrained to a change in photoperiod at different rates is also well established (Aschoff, [15a]). Because of this, it is important that animals be exposed to photoperiods for sufficient durations to allow entrainment and synchronization of various rhythms which may interact with, and influence, one another.

The rest-activity patterns of virtually every species studied have been shown to be strongly influenced by variations in photoperiod. Further, a substantial body of literature indicates that illumination schedules and light intensity specifically affect the placement, structure and duration of sleep (for a review, see [38]). For example, laboratory rats increase total sleep time by over an hour during constant light compared to baseline 12L/12D or DD values [39]. Similarly, in a marsupial, the kangaroo rat, sleep duration has been shown to be slightly lengthened under conditions of constant light [17]. In contrast, laboratory cats have been shown to decrease sleep time under conditions of constant light [159]. Sleep in some species of fish appears to be strongly inhibited

by constant light ([165], Tobler, unpublished data), while in at least one species, *T. tinca*, constant illumination appears to enhance sleep time [134].

Clearly, in the study of sleep duration the ideal photoperiod is the natural light-dark cycle. Just as evident is the fact that the use of alternative photoperiods is frequently unavoidable. Because of the necessity of constant illumination or of light/dim schedules in most observational studies, and in the interest of standardizing laboratory conditions during electrographic investigations, artificial photoperiods are typically employed. Surprisingly, the photoperiods employed are frequently not specified in the literature. The failure to report illumination schedules, as well as light intensity, often hinders the interpretation and comparison of sleep measures.

Effects of *ambient temperature* on sleep of laboratory animals has also been given considerable attention (for a review, see [127]). The primary result of changes in ambient temperature has generally involved variations in the structure of sleep, with sleep duration only slightly affected (e.g., [128], except at temperatures considerably below thermal neutrality [131,132].

Yet, substantial changes in sleep length have been reported in some nonlaboratory animals as a result of variations in ambient temperature. For example, due to a 7°C lowering of ambient temperature the average sleep duration in little brown bats declined by an average of 45% [41].

A further example is provided by Van Twyver's study [203] of seven alligators in which EEG changes initially thought to indicate sleep disappeared when ambient temperature was strictly controlled. As a result, the author concluded that these animals exhibited no sleep. Further, in a study in which perch were provided with a temperature gradient in the aquarium it was shown that the fish preferred a lower temperature at dawn and a higher temperature at dusk. A relationship was seen between locomotor activity and preferred temperature [144].

Failure to control ambient temperature then, especially in studies involving poikilotherms, may result in substantial alterations of sleep waking behavior and electrophysiological correlates. Because temperature may be such an important factor in the determination of activity in these animals, it has been suggested that a temperature gradient be provided in the experimental chamber to allow animals to self-select appropriate ambient temperature [53,120].

The influence on sleep duration of other factors such as *nutritional requirements*, *seasonal variations* and *age* have not been systematically or extensively examined. Yet there is preface evidence to suggest that each of these factors may affect sleep duration, at least to some degree. For example, in all domestic herbivores studied the availability and the type of food has been shown to influence, sometimes dramatically, sleep duration and placement [153,155]. Similarly, both the amount of food and feeding schedules have been shown to influence sleep placement and duration in cats [155,159].

Regarding *seasonal variations*, poikilotherms may be especially affected, as illustrated by reports that newts and salamanders [76] and certain species of fish [168] exhibit substantial variations in rest time as a function of season.

The few studies that have addressed the relationship between sleep and *age* in animals have been primarily concerned with sleep structure and not with length. Yet, the inverse relationship between age and sleep duration in humans is well established. This relationship has also been

shown in other mammals (e.g., [87, 89, 155]) as well as in at least one species of bird [162]. It is reasonable to assume that such a relationship may hold across phylogeny.

Finally, regardless of how well adapted an animal may be, reliable sleep length measures may be obtained only by recording or observing animals on a continuous basis for the duration of the entire photoperiod. The finding that factors such as cage sizes and complexity [49,51] and availability of cover [88,157] may affect the placement of sleep emphasizes the need for around-the-clock recording.

Because the sleep of many animals is polyphasic or may be displaced within the photoperiod as a result of laboratory conditions, methodology which necessarily involves extrapolation to obtain sleep length measures may yield misleading values.

To summarize, the reliability and validity of sleep length measures may be subject to question due to several factors. Disregard by researchers of the points mentioned above may substantially limit the utility of data presented. Failure to report elements of the experimental protocol makes it equally difficult to utilize these data for comparison within an evolutionary framework.

SUGGESTIONS FOR FUTURE RESEARCH

Of over 20,000 species of vertebrates (excluding about 20,000 species of fish) potentially available for study, the sleep durations of less than 200 have been delineated to date. As shown in Fig. 1, mammalian species constitute over half of the total number of species presented in the table, with the other four orders of vertebrates combining to constitute about 40% of the total. Invertebrate species have received virtually no attention. Clearly, and not surprisingly, studies of sleep duration in mammalian species are overrepresented relative to the order's proportional representation in the animal kingdom (59.3% vs. 8.9%). These species are generally more widely known, more easily obtained, and less difficult to maintain in the laboratory than are many species representing the other orders. As such, fish, amphibians and reptiles are all underrepresented to varying degrees.

Indeed, the percentages shown in Fig. 1 may be viewed as representing conservative estimates of the disproportionate attention given mammalian species. While it is not unusual to find several reports describing the sleep characteristics of a given mammalian species, virtually no species of reptiles or amphibians has been investigated by more than one laboratory. Taking this factor into consideration, the bias toward the study of sleep duration in mammalian species becomes even more extreme.

An additional weakness common to many studies, involving all species, is that frequently a small number of animals is used, thus restricting the degree to which results may be generalized.

It seems apparent then, that two avenues of research must be pursued. In order to provide a more reliable data base within a given species, more studies, using more animals, should be performed. Secondly, especially with regard to nonmammals, a wider variety of species must be studied. Only in this manner will it become possible to make meaningful statements regarding sleep duration among species and orders and to legitimately and fruitfully make comparisons between sleep duration and other ecological and constitutional variables.

Some approaches to the study of sleep, both in the laboratory as well as in the field, have been introduced in recent

years which may be useful in this endeavour. Particularly useful are techniques which may provide insight into the similarities or differences between rest and sleep, as these states are generally defined.

Because the resting state in invertebrates (and some amphibians and reptiles) has been difficult to classify in terms of standard electrographic criteria it may be valuable to correlate other changes in neuronal activity with behavioral manifestations of sleep or rest. The findings of Kaiser and Steiner-Kaiser [92] (see page 273) in the forager bee suggest that this method deserves consideration in other invertebrate and vertebrate species as well.

The method of EEG spectral analysis, frequently used in mammalian studies, should also be exploited in non-mammalian species. Indeed, Karmanova [94] has used this method to examine relationships between non-mammalian classes. However, in these studies the exact method of analysis is unclear and the analysis is confined to brief intermittent EEG samples. For the technique of spectral analysis to be effective continuous analysis is required in order to adequately describe and evaluate the evolution of the EEG across the sleep period. Such a procedure could aid in the delineation of electrographic activity which may correspond to behavioral sleep states in non-mammals.

Regarding behavioral evaluations of sleep and rest, the method of sleep (rest) deprivation is an alternative approach which may be useful in elucidating basic similarities between the resting state in nonmammals and the mammalian sleep process. For example, enforced activity during the usual rest periods of an invertebrate should elicit rebound effects similar to those observed after sleep deprivation in mammals, if these states serve a similar function. The approach has provided information regarding the nature of rest in cockroaches [191] and in fish ([165]; Tobler, unpublished data), allowing inferences to be made relative to the sleeplike quality of such states.

Another promising approach involves the use of time-lapse video recording. While this technique has typically been applied in animal studies as a means of corroborating electrographic indices of sleep (for example, [53]), recent investigations employing both human and animal subjects have demonstrated the value of time-lapse video alone as an index of sleep length. For example, the exclusive use of time-lapse has been employed to quantitatively assess changes in rest time in cockroaches and fish subsequent to rest deprivation ([191]; unpublished data) (see Fig. 2). The method may also be useful for long-term observation of non-laboratory animals housed, for example, under zoo conditions, or in "natural" settings [82].

In addition to video recording, radiotelemetry techniques may also be useful in characterizing sleep and wakefulness. The method has been successfully employed with laboratory rats [40] and monkeys [64, 142, 211]. The method has also been used to a lesser extent in the field with animals such as the tenrec, mountain beaver and hedgehog [170], with primates [29] and with some marine mammals [145]. Telemetry has also been utilized in the study of rest-activity rhythms by measuring physiological parameters such as heart rate (e.g., [62]). In summary, however, Allison's [4] prediction of a merging of laboratory and field traditions via the utilization of telemetric transmitters still appears far from being realized.

Recent technological advances have made it possible to store vast amounts of data efficiently and inexpensively. As a result, small lightweight activity-monitors may be em-

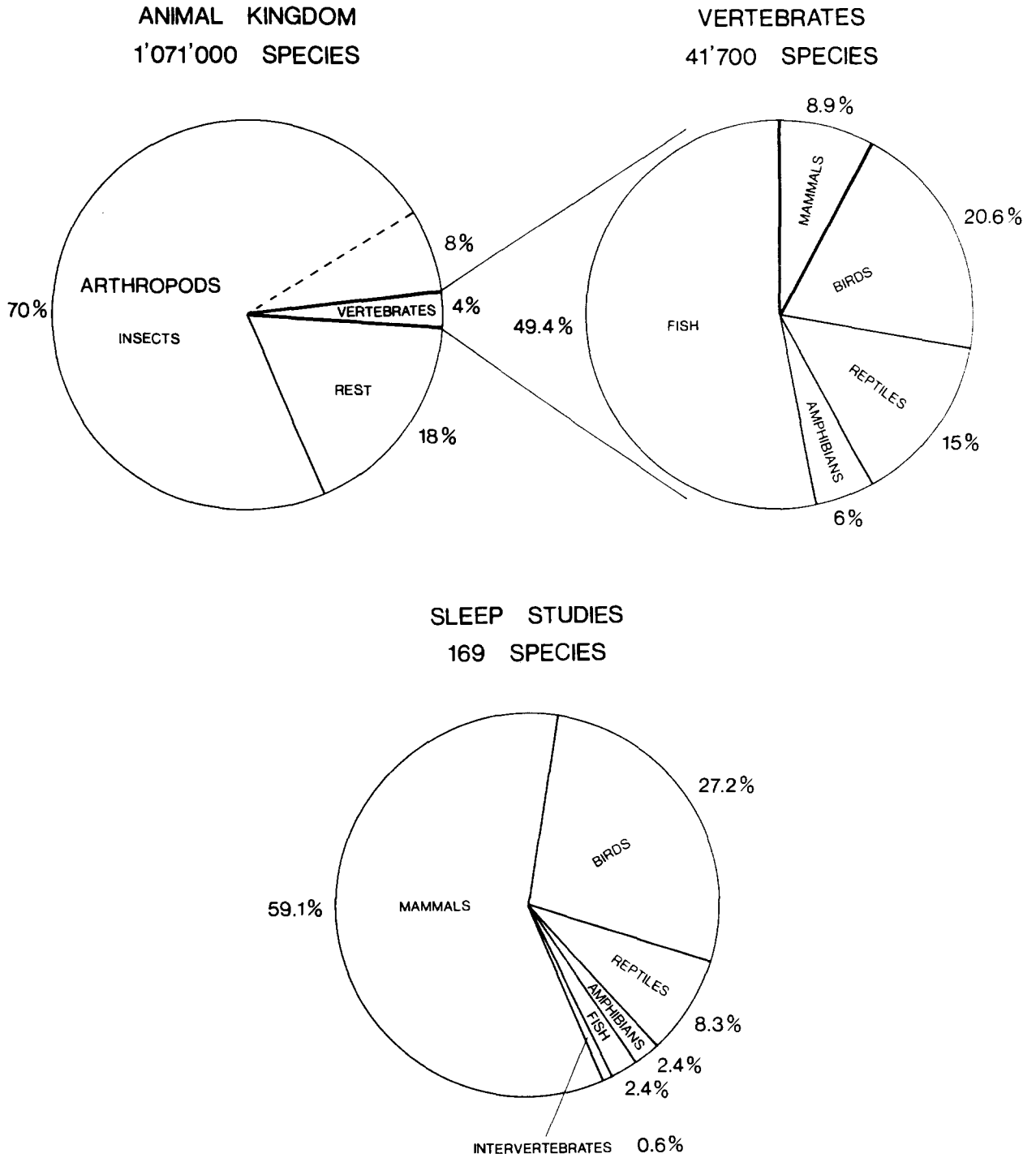


FIG. 1. Species representation in the animal kingdom (above) versus representation in studies addressing sleep duration (below).

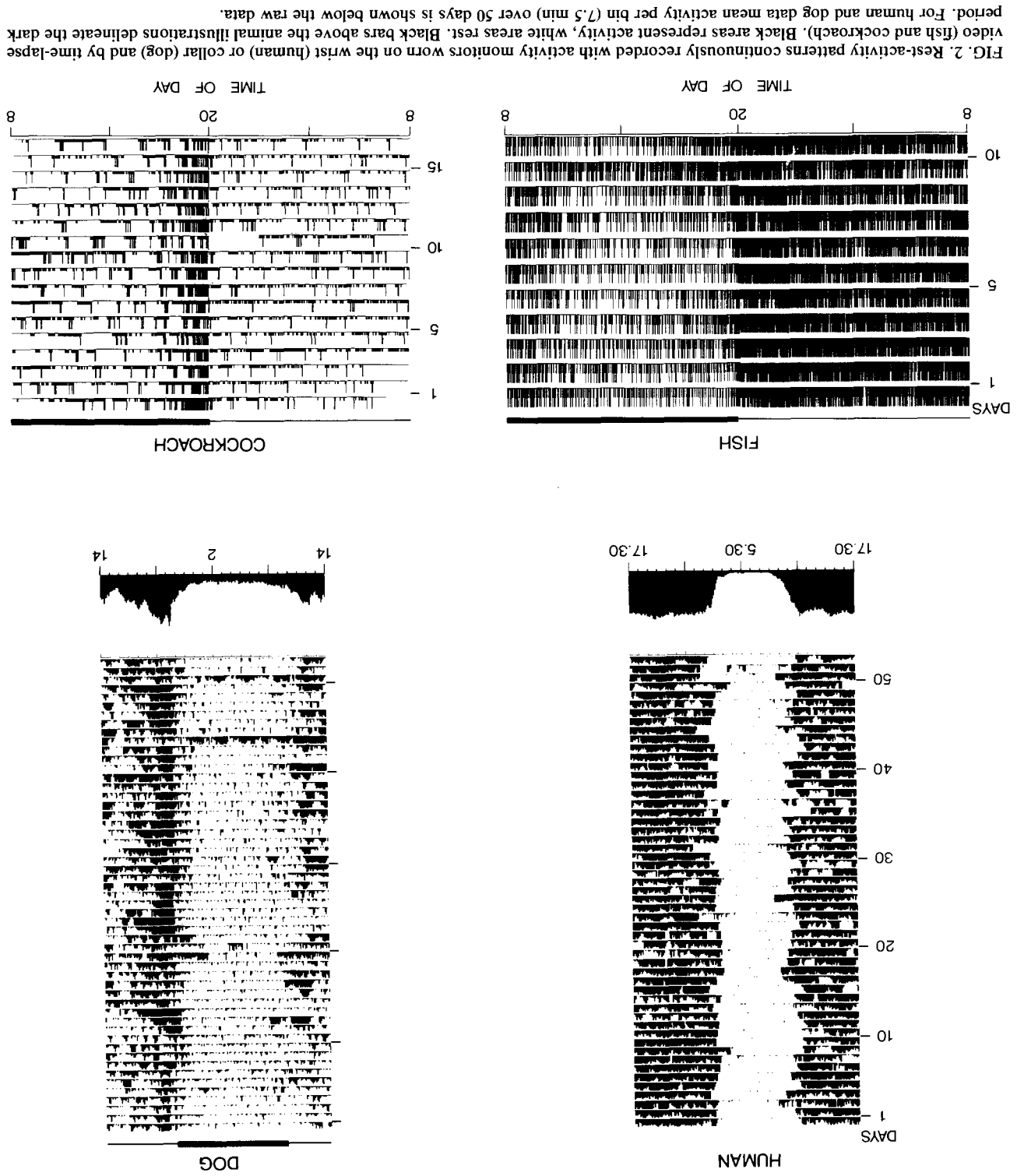


FIG. 2. Rest-activity patterns continuously recorded with activity monitors worn on the wrist (human) or collar (dog) and by time-lapse video (fish and cockroach). Black areas represent activity, white areas rest. Black bars above the animal illustrations delineate the dark period. For human and dog data mean activity per bin (7.5 min) over 50 days is shown below the raw data.

ployed to obtain long-term data on rest and activity in a wide variety of settings in a broad range of species. Figure 2 shows the type of data which has been obtained using such devices in dogs and in humans.

Perhaps due to difficulties in recording mechanics, or to keeping birds in restricted environments for prolonged periods, sleep length studies in birds have been few, and have typically used small samples.

Field studies of sleep in the herring gull have shown that eye closure ("blinking") is a good behavioral index of sleep in these birds [10,11]. The authors further suggest that there might be an association between depth of sleep and rate of blinking or amount of time that eyes remain closed. Also employing measures of eye closure, Lendrem [110,111] established a relationship between flock size, predatory danger and sleep in mallard ducks and barbary doves. The finding that there is a standard, easily measured behavioral index of sleep in birds is not only a valuable field technique, but also may provide a useful index by which to evaluate the effects of numerous variables on sleep. For example, using this measure Lendrem demonstrated in the barbary dove a decrease of eye blinking in response to sleep deprivation by presence of a predator.

With the previously described methods, in conjunction with traditional techniques, the examination of sleep duration may be broadened to include more species. In addition, by the use of both field and laboratory investigations, measures may be obtained under a broader range of environ-

mental conditions. These factors can only serve to enhance the reliability and validity of measures of sleep duration and placement.

In conclusion, it has been demonstrated that, at least in terms of behavioral criteria, the vast majority of animals thus far studied exhibit states of consciousness which may be defined as sleep. It is also evident (see Table) that different species exhibit variations in the amount and placement of sleep within the 24-hr day.

Traditionally, the examination of such variability in sleep length across species has been a principal feature of interest in the examination of sleep function. Yet, it is also clear from Fig. 1 that the data base upon which these comparisons are made remains sparse. This paucity of data continues to be the most important obstacle restricting the analysis of sleep duration measures in the effort to enunciate the functions of sleep. Sleep is ubiquitous across phylogeny and is manifested in many forms. Only by examining all forms of this behavior will it become possible to characterize sleep in terms of its evolutionary significance.

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