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Mammalian Sleep

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ABSTRACT

Knowledge about sleep comes primarily from research on mammalian species, whose daily sleep quotas range from 4 to 19 hours, with rapid eye movement (REM) sleep occupying 10% to 50% of this time. Findings of REM sleep or elements of it in monotremes have filled a gap in its evolutionary history. To some, this suggests that REM was inherited from reptiles, although the absence of REM in living reptiles casts doubt on this view.

The function of sleep remains controversial.¹ On one hand, restorative theories hold that brain processes during sleep sustain waking behavior (e.g., visual function, learning). On the other hand, the negative correlation of sleep quotas with body size across species suggests that sleep is a state of enforced rest most urgent in species with low energy reserves. Because most of the variance in sleep quotas remains unaccounted for statistically, supplementary theories are in order.

There are strikingly strong correlations of REM sleep quotas with degree of maturity at birth—that is, altricial species, born with a low percentage of adult brain weight after a short gestation period, have higher REM sleep quotas, whereas precocial species have lower quotas. Given other fetal characteristics of altricial species (e.g., lapse of thermoregulation), REM sleep may be a carryover from fetal life.

Most studies on sleep have been performed in mammals. Human beings, cats, rats, and, more recently, many mouse strains have been the most frequent subjects of sleep research, but about 100 other species have also been studied. There are at least two published reports about the daily sleep of mammalian species for each one pertaining to other classes.² This not only makes for mammal-centeredness in thinking about sleep but also affords the opportunity for extensive interspecies comparisons that can shed light on the purpose of sleep, which is still without adequate explanation. This chapter considers relevant theories in the light of available findings.

Despite their relative abundance, the mammalian data represent less than 3% of roughly 4260 extant species.

The belief that some mammals do not sleep (e.g., prey species, because of a need for constant vigilance; shrews, because of the need for incessant foraging) has been superseded by systematic observations. Some species, in some circumstances, may be able to postpone sleep for long periods, or sleep may simply be difficult to recognize, as in the ever-swimming, blind Indus dolphin, whose sleep occurs in periods measured in seconds as it contends with strong river currents.³

SLEEP CRITERIA

Sleep can usually be identified by sustained quiescence in a species-specific posture accompanied by reduced responsiveness to external stimuli, but a definition of mammalian sleep requires several additional criteria, such as quick reversibility to the wakeful condition and characteristic changes in the electroencephalogram (EEG). Quick reversibility distinguishes sleep from coma and hypothermic states (e.g., hibernation). With only minor exceptions, EEG changes reliably confirm sleep-related change in behavior and brain activity. Another fundamental property of sleep, derived from comparative studies in many species, is its homeostatic regulation. See Chapter 7.

These definitional criteria exhibit notable interspecies variation. Quiescence does not necessarily mean immobility; for example, some cetaceans reportedly swim while sleeping. In terrestrial mammals, lateral and sternoabdominal recumbency with eyes closed are the postures most commonly associated with sleep, but there are striking variations (Figs. 8-1 and 8-2). The horse, elephant, and giraffe, for example, sleep some while standing. Some species (e.g., cattle) sleep while they are ruminating, and many mammals can sleep with eyes semiopen. Choice of sleeping site is another element of species-specific sleep behavior and varies with mode of life and social organization. Burrows, caves, and trees are common sites because of the safety they afford, but some species (e.g., the zebra) sleep in the open and seem to rely on the presence of vigilant conspecifics for protection.⁵⁻⁸ Ritualistic presleep activity is characteristic of some species, ranging from the circling of a chosen spot (seen in dogs and foxes) to the construction of a nest each evening by chimpanzees.

Figure 8–1. Sea otter sleeping "moored" to a float of algae. (From Bourliere F: The Natural History of Mammals, 3rd ed. New York, Alfred A Knopf, 1967, p 68.)





Figure 8–2. Giraffe in a zoo, presumably in paradoxical sleep. (From Immelman K, Gebbing H: Schlaf bei Giraffiden. Z Tierpsychol 1962;19:84-92.)

These preparatory behaviors justify the description of sleep as appetitive, instinctive behavior.

The timing of daily sleep varies with the species and in each case is complementary to the activity pattern, which may be diurnal, nocturnal, crepuscular, or arrhythmic. Sleep tends to be concentrated in a single period each day in adult humans and the great apes, although the latter and people in many cultures take a midday nap. In most mammals, however, sleep is polyphasic, with sleep episodes interrupted by periods of wakefulness. Species also vary in the degree of responsiveness to external stimuli during sleep, some awakening more readily than others.^{9,10}

Sleep onset in mammals is associated with a slowing of EEG activity, a rising of EEG amplitude, and a decrease in muscle activity, followed in most species by the appearance of spindling activity, and in all cases culminating in sustained slow activity at relatively high amplitude. Spindling and slow waves are the hallmarks of mammalian quiet or non-rapid eye movement (NREM) sleep (the term NREM sleep is used synonymously with slow wave sleep [SWS] in nonhuman mammals).^{11,12} The characterization and quantitative analysis of sleep spindles in nonhuman mammals and their significance has received little attention. It is known that spindles are not merely a transition element in the EEG but that they occur also throughout NREM sleep. In some species, however, the distinction between wakefulness and sleep is not always clear-cut. Especially in carnivores, ungulates, and insectivores, there are frequent or protracted periods when spindles or slow EEG components appear sporadically against background behavioral activity that may not be clearly different from that of wakefulness. This characterizes the state commonly described as drowsiness, also referred to as "light sleep" or "spindle sleep." The transition from wakefulness to sleep depends on the derivation-in an occipital derivation, it is abrupt, whereas in the frontal derivation, it is gradual and can be subdivided into "light" and "deep" sleep.¹³ It should be noted that spindles in mammals are most apparent in frontal regions, but this does not mean that sleep there is more superficial.

Spindling activity varies from species to species; it occurs over a wide range of amplitudes and at a variety of frequencies (e.g., 11 waves per second in dogs, 6 to 7 Hz in the sloth, 8 to 11 Hz in the opossum, 10 to 16 Hz in rats, 10 to 13 Hz in mice, and 12 to 16 Hz in primates). Slow wave activity (SWA; 0.5 to 4 Hz) differs in its peak frequency depending on species—that is, it is more concentrated at lower frequencies in some species (human beings, rats) than in others (most mice). The considerable differences in amplitude between species are difficult to interpret because technical aspects of the recordings confound them. Although the changes in the EEG spectrum within NREM sleep, especially in SWA, are known to be continuous, NREM sleep is sometimes subdivided into "light" and "deep" sleep, on the basis of the amount of delta wave activity. In most primates, distinct features of the EEG have led to the definition of two stages in NREM sleep.

Another fundamental characteristic of mammalian sleep is its homeostatic self-regulation, which keeps the amount and depth of sleep in equilibrium with prior wakefulness. Sleep loss creates a debt that is repaid, in part, by some lengthening of subsequent sleep and, in addition, by the intensification of SWA, as indicated by its increased amplitude and density¹⁴ (see Chapters 7 and 33).

Mammalian sleep, as is well known, also includes paradoxical sleep (PS), or REM sleep, which is distinguished by desynchronized, low-amplitude EEG activity in association with eye movements, twitching of the extremities, and postural atonia. Eye movements vary in prominence and may even be absent, as in the mole. Detectability of atonia also varies. Rhythmic theta activity (4 to 8 Hz) originating in the hippocampus is a reliable indicator of PS and can be recorded in some animals with implanted epidural electrodes over the parietal or occipital cortex. Theta activity is less evident in frontal recordings. Many studies in mammals benefit from both recording sites by combining frontoparietal electrodes. Other striking features of PS are ponto-geniculo-occipital (PGO) spikes, cardiorespiratory irregularity, and largely inhibited thermoregulatory responsiveness.¹⁵ In all species, PS, defined by several of its behavioral components, is at its height in early life, either in the fetus or in the neonate. It is initially the predominant state-for example, occupying 90% of the kitten's first 10 days of life and perhaps even more time in the infant rat.16 By virtue of this pattern, PS has been considered ontogenetically primitive sleep, especially because PS time is reduced as electrophysiologic signs of quiet sleep and wakefulness emerge with maturation. However, recent studies investigating the development of EEG patterns in newborn rat pups have questioned this notion. The alternative view is that the vigilance state typical for newborns is a manifestation of the immature nervous system, which becomes progressively more organized and evolves simultaneously both into the typical EEG and behavioral manifestations of PS and into NREM sleep.¹⁷

The alternation of quiet sleep with periods of REM sleep constitutes the sleep cycle, also known as the NREM-REM (or REM-NREM) cycle, which can be considered the basic organizational unit of mammalian sleep (Fig. 8–3). Duration of the cycle varies widely from species to species, as do daily sleep quotas and the percentage of sleep time occupied by REM sleep. The cyclic organization of sleep is a characteristic shared by mammals and birds, which also share the behavioral and to some extent the EEG criteria of sleep. Notably, birds have a smaller difference in the EEG spectrum between wakefulness and NREM sleep than mammals. It is still an open question whether the bird brain that lacks the structures

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Figure 8–3. Twenty-four-hour distribution of non-rapid eye movement (NREM) sleep (N), REM sleep (R), wakefulness (W), and slow wave activity (SWA—i.e., "delta" power) in a C57BL/6 mouse and a Sprague-Dawley rat recorded in a 12-hour light, 12-hour dark cycle. Note the polyphasic sleep–wakefulness pattern (typical for all nonhuman primates) and the short NREM-REM sleep cycles of 12 to 15 minutes that are typical for small rodents.

responsible for generating slow waves has the capacity to respond to sleep pressure by increasing NREM sleep intensity. Because relatively little is known about avian sleep physiology, other unsuspected differences from mammalian sleep may exist. On the basis of current knowledge, however, what chiefly distinguishes avian from mammalian sleep is the much lower percentage of REM sleep in birds (about 5% of sleep time, on the average, as opposed to 15% to 30% in mammals), the occurrence of REM sleep in clusters, the much briefer REM periods (often less than 10 seconds), and the correspondingly short sleep cycles. It should be noted, however, that there is an immense diversity of bird species, of which few have been recorded.

EVOLUTIONARY HISTORY

The essential similarity of sleep in birds and mammals may well be a clue to the history and function of sleep.¹⁸ The sleep cycle first appears in evolutionary history in association with endothermy, which is the maintenance of a high, constant body temperature by metabolic means, as found only in birds and mammals, enabling them to occupy nocturnal niches and survive in cold climates. The alternation between REM and NREM states has yet to be explained, but it is possible that the cycle evolved independently (in parallel) in birds and in mammals, or in their immediate forebears (mammal-like reptiles) (Fig. 8-4). Research on living reptiles has not produced convincing evidence of REM sleep or of sleep organization that might suggest a cycle. Although some studies of reptiles have claimed to see evidence for eye movements and EEG changes during quiescent periods, it remains unclear whether these phenomena were simply transient awakenings or REM sleep.¹⁹ Brain structure and sensorimotor organization in reptiles differ greatly from those in birds and mammals, so it is difficult to draw conclusions about reptilian sleep based on simply observing the electrical activity from screw electrodes positioned on the skull, as can be done in mammals.

However, studies of mammals have localized the neurons driving and responding to REM sleep processes to the brainstem, and these neuronal groups appear to be present in reptiles (see Chapter 10). This can be taken advantage of by recording from these neurons during active and quiescent



Figure 8–4. Temporal relationships and lines of descent for birds, mammals, and reptiles. *Solid lines* indicate availability of fossil record; *dotted lines* indicate still-uncertain relationships.

states in reptiles. In the first study using this approach, the neuronal activity of the midbrain and pontine regions responsible for REM sleep generation was studied in the turtle.²⁰ This study found no evidence of cyclicity in neuronal activity during extended quiescent periods and hence no evidence of REM sleep. It would be extremely valuable to confirm these results in other reptilian species. Pending such evidence, these data suggest that REM sleep may not have existed in reptilian species but may have evolved rapidly with endothermy.

A striking finding of the study in turtles was that most brainstem neuronal activity in the observed portions of the midbrain and pontine reticular formation decreased to minimal levels, often completely ceasing, within seconds after movement. In contrast, most brainstem cells in the same brain regions of mammals show tonic activity even during quiet waking. This tonic waking activity presumably allows for more rapid response to sensory inputs. One can speculate that tonic waking activity is accompanied by the need for the inactivity–activity cycle that accompanies mammalian sleep.

Belief that the emergence of PS was relatively recent was encouraged by its reported absence (although quiet sleep was present) in the Australian short-nosed echidna,²¹ one of the three surviving monotremes (egg-laying mammals) that diverged early from the main paths of mammalian evolution (see Fig. 8–4). It may seem that some characteristic of the echidna (mode of reproduction, fossorial adaptation, or low body temperature) obviates the need for PS and explains its absence, but this is not the case. The presence of PS in birds shows that it is not related to viviparity. PS is clearly present in other fossorial mammals (e.g., the mole and blind mole rat) and in species with very low body temperature (e.g., the sloth).

Need for qualification of the belief that PS is absent in the echidna is indicated, however, by a finding that, at some times when the echidna's EEG indicates quiet sleep, there are bursts of neuronal activity in its brainstem similar to activity characteristic of REM sleep in therian mammals.²² This is said to indicate that REM and NREM sleep did not evolve sequentially but as a differentiation of a primitive state that held the seeds of both sleep states. Furthermore, there is now unequivocal evidence of REM sleep in another of the three surviving monotremes, the platypus, occupying 6 to 8 hours per day (more than in any other mammal) and accompanied by eye movements, atonia, twitching, and an elevated response threshold, as generally found in mammalian PS, although with EEG voltage that may be at a level characteristic of quiet sleep in eutherian mammals.^{23,24}

Complicating speculation about the history of PS are reports of its absence in the bottle-nosed dolphin and the common porpoise, which cannot be considered primitive mammals^{25,26} (see Chapter 10). Most NREM sleep in these species is unihemispheric, consisting of synchronized, slow activity in one cerebral hemisphere and desynchronized activity characteristic of wakefulness in the other. There is no bilateral high-amplitude (delta) sleep. This sleep organization seems necessary to guarantee respiratory function.²⁷ It has been suggested that PS is also absent on this account, although it is present in the northern fur seal²⁸ and the manatee,²⁹ both of which also have unihemispheric sleep. Other reports make it advisable to reserve judgment regarding the absence of PS in any cetaceans. Its possible presence is suggested by a report of quiescent hanging behavior accompanied by twitching in captive beluga whales.^{30,31} Penile erections have been reported in the absence of overt sexual behavior in the bottle-nosed dolphin.³² However, as myoclonus is seen in terrestrial mammals in NREM sleep³² and nocturnal erections are not always linked to REM sleep in terrestrial mammals,³³ it is unclear whether these observations indicate REM sleep in cetaceans. Unequivocal REM sleep, as identified by EEG and electromyographic (EMG) recording and evidence of elevated arousal thresholds, has not been demonstrated in any cetacean. Even if the twitches that have been observed are eventually demonstrated to be signs of REM sleep, a mystery remains. The maximal number of twitches seen in cetaceans during relatively quiescent periods is of the order of 10 to 20 per day, clustered in two or three short time periods.³¹ In terrestrial mammals such as the rat, visual scoring of twitches as has been done in cetaceans registers thousands of twitches each day, most in REM sleep (J. M. Siegel and O. I. Lyamin, unpublished observations). Therefore, even if the twitches in cetaceans mark a REM sleep-like state, the amount of REM sleep in cetaceans would be the lowest among the mammals. Further investigations of cetacean sleep aimed at addressing the question of the amount and nature of REM sleep-like phenomena might provide fundamental insights into the evolution and function of REM sleep.

COMPARATIVE THEORIES

The emerging evolutionary perspective has undermined the previously dominant influence of commonsensical restorative theory, which holds that sleep is for relief of bodily or cerebral deficits caused by waking activity. Restorative theory cannot readily explain the dramatic interspecies variation in daily mammalian sleep quotas (Table 8–1). (For a comprehensive compilation, see *Principles and Practice of Sleep Medicine*, first edition, pp. 39-41. See also Zepelin and Rechtschaffen,³⁴ Meddis,³⁵ and Elgar et al.^{36,37}).

Inspired by this variation, comparative theories have been advanced as alternatives. Guided by an assumption that sleep varies with complexity of the brain, some of these assert that sleep has cerebral functions. PS has attracted interest in this respect because of its cerebral activation. For example, taking note of instinctive behaviors (e.g., rage) released during PS in cats whose postural atonia is surgically abolished, Jouvet³⁸ suggested that PS evolved for daily reprogramming of innate behaviors to preserve them in species that rely chiefly on learning. This view is attractive as an explanation for the absence of PS in reptiles and its meagerness in birds, which rely heavily on instinctive behaviors. On the other hand, if the theory is correct, PS quotas should be greatest in mammals with the most learning ability (e.g., primates), but as can be judged by the data in Table 8–1, this is not the case.

In what can be called the eraser theory of REM sleep, Crick and Mitchison have treated its reported absence in the echidna as evidence that it amounts to a mechanism for *reverse learning*, in which stimulation of the forebrain weakens the synaptic strength of undesirable "parasitic modes" of neuronal activity, thus fine-tuning the brain's operation.³⁹ The echidna, it is said, gets by without REM sleep because its surprisingly large neocortex makes reverse learning unnecessary. If true, an inverse relationship between size of neocortex and REM sleep quotas is to be expected in other species, but supportive data are lacking.⁴⁰ Human total sleep time, REM sleep, and percent of sleep time spent in REM sleep are not unusual. Other mammals have much higher or lower amounts of each state.

Table 8-1.Daily Sleep Quotas in a Sample of Mammalian Species				
Species	Total Daily Sleep Time* (hr)	Daily REM Time (hr)		
Echidna	8.5	?		
Platypus	14.0	7.0		
Opossum	18.0	5.0		
Koala	14.5	?		
Mole	8.5	2.0		
Bat	19.0	3.0		
Baboon	9.5	1.0		
Humans	8.0	2.0		
Armadillo	17.0	3.0		
Rabbit	8.0	1.0		
Rat	13.0	2.5		
Hamster	14.0	3.0		
Dolphin	10.0	?		
Seal	6.0	1.5		
Guinea Pig	9.5	1.0		
Cat	12.5	3.0		
Ferret	14.5	6.0		
Horse	3.0	0.5		
Elephant	4.0	?		
Giraffe	4.5	0.5		

Values are rounded to the half hour and exclude drowsiness. Some values are averages for two or more members of the same genus.

*Total daily sleep time includes daily REM time.

REM, rapid eye movement; ?, reported absence of REM sleep or uncertainty.

This poses a problem for sleep-learning or "information processing" theories of sleep function.⁴¹

ENERGY CONSERVATION

A major alternative to restorative theory is the view that mammalian sleep is for energy conservation, as suggested by its association with endothermy. Two versions of this view are frequently mistaken to be the same. One of these, advocated by Berger⁴² and coworkers, holds that sleep is for reduction of energy expenditure below the level attainable by rest alone. Interdependence of quiet sleep and endothermy is inferred from their concurrent maturation in mammalian infancy and the uninterrupted operation of thermoregulatory processes during quiet sleep at a reduced temperature level.42,43 The reduced capacity for thermoregulation during PS (see Chapter 24) is considered evidence that PS is a vestige of a reptilian state of ectothermic inactivity. The notion that quiet sleep, torpor, and hibernation are related dormant states with a common purpose, mainly energy conservation, is not upheld by recent data (see Chapter 7). The upsurge and intensification of SWA directly following bouts of torpor or hibernation suggest compensation for loss of sleep during the hypothermic bouts.⁴⁴⁻⁴⁶ The metabolic expense of heating the body toward euthermia in the periodic interruptions of hibernation is close to the energy saving that results from the immobilization and lower temperature during hibernation.

Above all is the question of whether reduction of metabolic rate is sufficient as the raison d'être for sleep. At most, sleep

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could effect a metabolic saving of about 15%,47 and the savings would largely depend on the animal's nutrition⁴⁸ and its capacity to remain in quiet wakefulness. There are some species with high sleep quotas and low metabolic rates, a condition traceable to energy-deficient diets.⁴⁸ An outstanding example is the endangered koala (see Table 8-1), whose diet consists of rare types of eucalyptus leaves with low nutritional value.⁴⁹ Other examples are edentates (e.g., the sloth) and armadillos. Such species cannot afford high activity levels. Their extended sleep seems necessary to ease metabolic pressure and is consistent with a role for sleep in energy conservation. In humans, the overnight saving is more likely to be only 5% to 11%, taking into account the effects of body movement and arousals.⁵⁰⁻⁵² An argument against the view that sleep is for energy conservation enforced by rest is the reported continuous movement of dolphins while asleep.³ This is considered evidence of some sleep function other than enforced rest.

Correlational Findings

The second version of energy conservation theory considers the reduction of metabolic rate during sleep to be of minor importance. The principal contribution of sleep (with no qualification regarding PS) is held to be the enforcement of rest so as to set a limit on activity and energy expenditure. This view emerged from Zepelin and Rechtschaffen's³⁴ comparative study of sleep parameters, potential life span, and other constitutional variables in 53 mammalian species. The study assessed a long-standing belief that species with high daily sleep quotas have relatively long potential life spans because they benefit from lowered metabolism during sleep. The contrary proved to be the case: long-sleeping species are typically short-lived. They also tend to be small in size and high in basal or resting metabolic rate per unit of body weight. There was an impressive correlation (0.63) between sleep quotas and metabolic rate.⁵³ Together with knowledge that the metabolic cost of physical activity varies inversely with body size⁵⁴ and that daily food requirements relative to body size are disproportionately high in small mammals,55 the finding on metabolic rate led to the conclusion that sleep sets a limit on energy expenditure to the extent necessary to balance a species' energy budget.

Table 8–2 summarizes relevant correlations found in updated analyses of EEG and behavioral sleep data for 85 taxa (species or genera), with missing data for some taxa in each analysis. Despite recent revisions in the sleep data (Asian elephant,⁵⁶ giraffe⁵⁷), added data for newly studied species (koala,⁵⁸ ferret⁵⁹), and some adjustments and expansion of the data for constitutional variables, the results are quite similar to previous findings. Previous and present correlations of body weight, brain weight, and encephalization quotient with total daily sleep time and cycle length are virtually identical. Consistency was somewhat less for correlations of metabolic rate and the correlations of PS measures. Correlations of quiet sleep time differed most from previous findings. This was because the present analyses made no adjustment of sleep quotas for drowsiness.

Analyses of partial correlations found, as in previous research, that brain weight and cycle length were positively correlated independently of body weight (r = .64; P < .001), but body weight and cycle length did not correlate independently, thus leaving brain weight alone as a likely determinant

Table 6–2. Cori	relations between sie	ep Parameters a	and Constitutional	variables	
Constitutional Variables	Total Daily Sleep Time (hr)	Quiet Sleep Time (hr)	Paradoxical Sleep Time (hr)	Paradoxical Sleep (%)	Cycle Length
Body weight	53*	53*	45*	12	.83*
	(85)	(65)	(65)	(65)	(33)
Brain weight	55*	48*	52*	25	.89*
	(71)	(56)	(54)	(56)	(32)
Metabolic rate	33†	.30 [‡]	.13	09	82*
	(65)	(51)	(50)	(50)	(29)
Encephalization	17	10	20 [†]	30 [‡]	.52†
quotient	(69)	(55)	(53)	(55)	(32)

Common logarithmic transformations were used for the constitutional variables. Log (1 + X) transformations were used for paradoxical sleep values. Number of cases per coefficient is in parentheses.

*P < .001

 $^{\dagger}P < .01$

[‡]P < .05

of cycle length. Brain weight and body weight both failed to correlate with sleep time independently of each other, as was found in a previous set of analyses.⁶⁰ It therefore seems best to consider the correlations of sleep time with brain weight and body weight, without distinction between them, as consequences of *body size*. Multiple regression analysis showed that brain weight and body weight together (i.e., body size) could account for 31% of the variance in sleep time.

Findings similar to those discussed earlier were obtained by Elgar et al.^{36,37} in a study based solely on electrographic sleep data for 69 species, with family as the unit of analysis. Agreement between the two sets of findings is important because the choice of families as the taxonomic level for analysis guards against possible inflation of sample size owing to similarities between species with shared phylogenetic backgrounds.

The correlation findings underwrite the view that sleep occurs to enforce rest and keep energy expenditure at an affordable level. There may be less pressure for sleep in large species because of their greater energy reserves. The proportion of fat to body mass increases with size, ranging from less than 5% in the smallest mammals up to 25% to 30% in species weighing 1000 kg.55 As body size increases, the ratio of surface to body mass decreases and thickness of fur increases. Large mammals consequently have lower thermal conductance (flow of heat to the environment) and wider thermoneutral zones. This lessens requirements for active heat production to maintain body temperature. Lindstedt and Boyce,60 as illustrated by Figure 8-5, have shown that fasting endurance (survival time) at thermoneutrality is a function of body size, and the size advantage is accentuated in the cold. Even at thermoneutrality, as the figure shows, survival time is short for small species. Many are frequently only hours away from death by starvation. They may require more sleep to avoid exhaustion of energy reserves. Also consistent with an energy conservation role are the relatively high sleep quotas that all mammals have early in the maturational period, when energy must be channeled into growth.

This version of energy conservation theory befits the requirements of endothermy, which is not only for thermoregulation alone but also for the increased aerobic capacity required for sustained running, climbing, and other vigorous activities. A mammal's basal energy requirement is at least five times that of an ectotherm similar in size and body temperature.⁶¹ This theory is also in accord with findings on prolonged sleep deprivation in rats. With ultimately fatal consequences, the rats suffered from increased metabolism, as shown by weight loss in spite of increased food intake, along with reduced body temperature in spite of increased metabolic rate. Prolonged deprivation of REM sleep alone has similar effects.⁶²⁻⁶⁴ These findings indicate



Figure 8–5. Fasting endurance (or survival time) as a function of body size for mammals. The *top line* represents survival time at thermoneutral ambient temperature, where $t_s = 9.30 \text{ M}_b^{0.44}$. *Steeper lines* represent survival times at elevated metabolism induced by cold. (From Lindstedt SL, Boyce MS: Seasonality, fasting endurance, and body size in mammals. Am Nat 1985;125:873-878. The University of Chicago Press. All rights reserved.)

an indispensable role for sleep in energy regulation, as suggested by the relationships of sleep quotas and constitutional variables. The convergence here of experimental and correlational findings is theoretically promising.

Immobilization Theory

Because correlational findings in support of energy conservation theory fall short of explaining even half of the variance in sleep quotas, the way is open for other viewpoints. Restorative theories having failed to explain species differences, behavioral theories have come to the fore, expanding the concept of sleep as a state of enforced rest. It is suggested, for example, that large mammals sleep relatively little because they require extra time for foraging.⁶⁵ A related view is that the function of sleep amounts to adaptive nonresponding, 35,65 meaning that it prevents activity (e.g., foraging) when it would be dangerous or inefficient, and it blocks harmful reactions that might occur in an animal merely resting but aware of ongoing events. Meddis³⁵ (p. 54) elaborated, "The benefits of sleep depend upon the species. For some the conservation of energy is most valuable, for others, the protection from predation... for others, the timing element." In effect, however, such theory is untestable, for there will always be some need that sleep can be said to meet. Filling spare time can be considered a function of sleep. But how much spare time does a species have? With circular reasoning, it is argued that time in sleep is a measure of spare time (Fig. 8-6).

ECOLOGIC INFLUENCES: THE ALTRICIAL–PRECOCIAL DIMENSION

It is often assumed that species differences in sleep reflect environmental influences, but this is not readily apparent. Probably the clearest case of an ecologically determined characteristic is the unihemispheric sleep found in some marine mammals. Drowsiness in some species seems to have an ecologic basis. Its prominence in ungulates (e.g., the horse) may be a compromise between sleep and alertness to predatory threat. On the other hand, there is no simple explanation for the prominent drowsiness of carnivores (e.g., the cat), which seems like purposeless fraying of sleep.

Predation is the ecologic variable that has attracted most interest. Because of the scarcity of data on the extent to which individual species are subject to predation or have suffered from it in their evolutionary past, judgments of its influence are open to question. Findings by Allison and Cicchetti,⁶⁵ however, raised the possibility that PS quotas are reduced by predatory threat because the elevation of sensory thresholds during PS puts prey at a disadvantage.

Relatively neglected in ecologic theorizing about sleep is the role of species differences in reproductive strategies and life histories. Adaptation to the environment occurs not only through fine-tuning of physical and behavioral characteristics but also through changes in the number of offspring and the timing of their maturation. Interspecies variation in sleep may be secondary to such adaptations. Commanding attention in this respect is the variation of REM sleep with maturational variables, as illustrated in Figures 8–7 and 8–8.

In *precocial species*, that is, those born fairly mature (e.g., the guinea pig, sheep), the REM sleep percentage at birth is low and near the adult level. In *altricial species*, that is, those born immature (e.g., the rat, the cat), the REM sleep percentage is initially high and remains relatively high even after maturation.¹⁶ Also indicative of influence by maturational timing is the inverse correlation of REM quotas with gestation time.^{34,36}

Previous findings of correlation between daily REM sleep time and degree of maturity at birth were confirmed with expanded data for up to 65 viviparous species or genera (echidna and platypus excluded). For eutherian mammals,



Figure 8–6. Nine African lions share a ribbon of shade and sleep in the heat of day. (From Schaller GB: Life with the King of Beasts. Natl Geog 1969;135:494-519. By permission of Dr. George B. Schaller. Copyright 1969, National Geographic Society. All rights reserved.)



Figure 8–7. Maturational changes in rapid eye movement (REM) sleep as a percentage of total sleep time in two altricial species (rat and cat) and a precocial species (guinea pig). (Reprinted from Jouvet-Mounier D, Astic L, Lacote D: Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. Dev Psychobiol 1970;2:216-239, by permission. Copyright 1970, John Wiley & Sons.)



Figure 8–8. Daily rapid eye movement (REM) sleep time in adult mammals as a function of neonatal maturity, represented by the percentage of adult brain weight in neonates of the same species.

the four-point altricial-precocial (A-P) ratings were assigned previously by an expert mammalogist without knowledge of the sleep data (Table 8–3). For this analysis, the author gave marsupials a rating of 1 based on the criteria of the scale. The results, shown in Table 8–4, were independent of body weight and brain weight and differed from previous findings chiefly in terms of a significant correlation in the present research between the PS percentage and the gestation period. It is noteworthy that in the four marsupial species, the two with the shortest gestation periods had PS quotas and percentages radically higher than the others—the highest in the entire sample. The recent findings in the platypus strengthen these correlations, as these animals are highly immature at birth

and they have the highest amount of REM sleep time of any
animal yet studied. The absence or minimal presence of PS
in cetaceans is understandable on the basis of their extreme
precociality.

These analyses also found a correlation of .49 (P < .001) between daily quotas of PS and quiet sleep. In the 49 species with complete data, this correlation with body weight and

able 8–3.	Altricial–Precocial Scale for Neonates of Viviparous Species	Me Ma Rep Var
cale Value	Description	Alu
1	Eyes closed; naked; rolls; sometimes can	Neo
2	Eyes barely closed or just open; furred;	Ges
2	crawls well (2.5: eyes open; can cling)	Litte
4	Eyes open; furred; can walk and	
	follow or swim	To n
ntermediate scale values (e.g., 2.8) were assigned to some		v t
species		 t

 Table 8-4.
 Correlations of Paradoxical Sleep

 Parameters with Measures of Neonatal

 Maturity and Reproductive Variables

Maturity and Reproductive Variables	Paradoxical Sleep Time (hr)	Paradoxical Sleep (%)
Altricial-precocial rating	66*	45 [†]
	(65)	(64)
Neonatal brain weight (%)	61*	55†
	(27)	(27)
Gestation period	.63*	39†
·	(60)	(59)
Litter size	.51*	.41 [†]
	(63)	(62)
To minimize skewness, commo	on logarithmic tra	insformations

were used for gestation period and litter size. Log (1 + X) transformations were used for paradoxical sleep values. Number of cases per coefficient is in parentheses.

*P < .001 †P < .01

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Adapted from Eisenberg JF. The Mammalian Radiations.

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brain weight partialed out was .28 (P < .05). These results are consistent with the view that PS provides endogenous stimulation to the brain to promote recovery from sleep.⁶⁶

The striking relationships between REM quotas and neonatal characteristics give no clear indication of the maturational events that are responsible. If one adopts Parmeggiani's⁶⁷ view that REM physiology is under rhombencephalic regulation (as opposed to the hypothalamic regulation in the rest of sleep), then maturation of the hypothalamus may be the critical factor. Given the expression of fetal characteristics (lapse of thermoregulation, respiratory irregularity, and twitching) in REM sleep during maturity, REM sleep could be considered a carryover from fetal life. The difference between mammals and birds in the representation of REM may well be explained by unidentified differences between them in maturational timing.

The association of REM with altriciality takes on added significance with the realization that reptiles are strictly precocial and that altriciality evolved in birds and mammals in conjunction with endothermy. Evolutionary theorists agree that the metabolic cost of endothermy favored altriciality, which meant the birth of exothermic rather than endothermic young. One view is that altriciality reduced the energy requirements for maturation by placing reliance on parental body heat for temperature regulation in the young, allowing their food to be channeled primarily into growth.⁶⁸ Another view is that altriciality mainly allowed greater flexibility in meeting energy requirements by shortening gestation and incubation periods, putting off much of the expense of propagation until after birth, thus splitting the expense between parents, both of whom could then forage for the young.⁶⁹ Precociality in some mammals evolved as a later adaptation.

Rather than outright inheritance from reptiles, as the finding of REM sleep in the platypus has suggested to some writers, REM sleep seems to be part of the evolution of endothermy, which distinguishes mammals from reptiles. It is simultaneously part of the transition from the strict precociality of reptiles. The limited indications of REM sleep features in the echidna are evidence of this transitional origin as opposed to straightforward inheritance from reptilian forebears.

SUMMARY

Evolutionary history suggests that mammalian sleep developed in association with endothermy, paralleling a similar development of sleep in birds. Consistent with this impression are several clusters of correlated variables that must also be taken into account in theorizing about the function of sleep. One is the correlation of daily mammalian sleep quotas with body weight and weight-specific metabolic rate, indicating greater requirements of sleep in species with low energy reserves. Another is the correlation of REM sleep parameters with A-P status, gestation time, and litter size, indicating the influence of maturational timetables on the prominence of REM sleep and suggesting that it is a byproduct of altriciality and endothermy. Less clearly related to endothermy is the positive correlation of the NREM-REM cycle length with brain weight, a relationship that is also apparent in the increase of cycle length with maturation in mammals. On the basis of an old comparative study that showed a high correlation of mammalian brain weight with cortical acetylcholine content and cholinesterase activity,⁷⁰ it could be speculated that cholinergic mechanisms known to influence cycle length are probably its operative link with brain weight.⁷¹

Clinical Pearl

Although many sleep parameters differ between species, human sleep does not appear to be qualitatively unique. This factor makes animal models suitable for the investigation of many aspects of sleep pharmacology and pathology.

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