

Sleep in mammals

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Abstract. Quiet sleep (QS) was correlated with a different set of constitutional variables from those associated with active sleep (AS), in a sample of 69 species of mammals. The time spent in quiet sleep was negatively correlated with body size and basal metabolic rate. The latter relationship remained even after controlling for the effects of body weight. Neither the total time spent in active sleep, nor active sleep as a percentage of total sleep time was significantly correlated with body weight or metabolic rate. Altricial species spend more time in active sleep than do precocial species. The time between the onset of successive episodes of active sleep, the AS–QS cycle length, was positively correlated with body weight. For their body sizes, species that live in temperate regions have shorter AS–QS cycles than those living in tropical or sub-tropical regions. Correlations between patterns of sleep and adult brain weight probably result from the confounding effects of body weight. These findings were used to evaluate several explanations for interspecific differences in patterns of sleep among mammals.

Birds, mammals, and maybe even reptiles, have some form of daily sleep (Campbell & Tobler 1984). Among mammals the amount of time recorded sleeping each day varies from 3 or 4 h in the horse, *Equus caballus* (Ruckebusch 1972) to over 20 h in the pocket mouse, *Perognathus longimembris* (Walker et al. 1983).

Variation in daily sleeping time and in patterns of sleep among mammals has been attributed to species differences in the need to conserve energy (Walker & Berger 1980), to species differences in predation risks (Allison & Cicchetti 1976; Meddis 1983), and to the amount of time different species need to acquire energy through foraging (Allison & Cicchetti 1976). In this paper we use comparative relationships between sleep measures, morphology and physiological processes to test these evolutionary explanations for taxonomic differences in patterns of sleep among mammals.

Sleep is comprised of slow wave or quiet sleep (QS) and rapid eye movement or active sleep (AS). Most of the sleeping period typically consists of quiet sleep which is characterized by behavioural and autonomic nervous system quiescence, and by high-amplitude slow waves, as measured by electroencephalogram (EEG). Active sleep is characterized by brief movements of the extremities, facial muscles and, especially, the eyes, and by shorter periods of low-amplitude waves on EEG record-

ings. A typical mammalian sleep pattern consists of quiet sleep interspersed with active sleep episodes.

The amount of time a mammal spends asleep each day may have evolved as a means to conserve energy. One of our interests is to test the idea that cross-species variation in the amount of time spent in quiet sleep reflects varying needs to conserve energy. Mammals are immobile during sleep and energy expenditure is reduced. Walker & Berger (1980, page 260) argued that if quiet sleep 'evolved to offset increased metabolic costs of endothermy, mammals with high metabolic rates might be expected to sleep more than those with low metabolic rates'. Metabolic rates per unit of body weight are higher for smaller mammals, leading to the prediction that smaller animals should sleep more. Comparative studies of sleep by Zepelin & Rechtschaffen (1974), Walker & Berger (1980) and Meddis (1983) yielded results consistent with this prediction: both total sleep time and quiet sleep time were negatively correlated with body size, and positively correlated with mass-specific metabolic rate (total metabolic rate divided by body mass).

However, the same comparative relationships among body size, metabolic rate and sleep would arise if larger animals have less time to sleep because they must spend more time foraging to meet their higher total energy requirements (see Allison & Cicchetti 1976). To discriminate between the energy conservation and foraging time hypotheses, the relationship between metabolic rate and sleep variables must be assessed independently of

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size. For a given size, the energy conservation hypothesis predicts that increasing metabolic rate will be associated with more sleep. The foraging time hypothesis, on the other hand, predicts that for a given size sleep time will decline as metabolic rate increases.

Active sleep, whatever its benefits, may pose at least two kinds of costs to mammals. First, thresholds for arousal are elevated during active sleep, potentially increasing the risk of predation (Allison & van Wyver 1970a; Allison & Cicchetti 1976; Amlaner & McFarland 1981). Second, thermoregulation is thought to be less effective during active sleep, putting animals at risk from heat loss or gain (Glottzbach & Heller 1976; Parmeggiani 1977; Schmidek et al. 1983). Most mammals sleep in environments where temperatures are below body temperature. Thus, smaller mammals with high surface to volume ratios and high metabolic rates for their body sizes may be more vulnerable to heat loss during active sleep. Such species might therefore have evolved less total active sleep, or shorter active sleep episodes to reduce heat loss at any one time. Alternatively, this relationship might not be found if small mammals are able to reduce heat loss by sleeping in nests or burrows, or huddled together in groups.

Whether smaller species have evolved less active sleep to avoid heat loss is difficult to evaluate from the published evidence. Contrary to the heat-loss prediction, Zepelin & Rechtschaffen (1974) found that the amount of time spent in active sleep was positively correlated with mass-specific metabolic rate. But this relationship may have arisen because the time spent in active sleep correlates positively with time spent in quiet sleep in mammals, and smaller mammals sleep more overall. Zepelin & Rechtschaffen (1974) did, however, find a negative relationship between the length of the AS-QS cycle and mass-specific metabolic rate: mammals with high mass-specific metabolism had much shorter AS-QS cycles (see also Meddis 1983). These latter results suggest that small animals may avoid long episodes of active sleep and thereby reduce the amount of heat loss during any one period, while maintaining their total amount of active sleep. But the use of mass-specific metabolic rate in these studies makes it difficult to separate metabolic rate effects from body size effects. A more direct test of the heat-loss hypothesis would investigate whether mammals with high metabolic rates for their size avoid long episodes of active sleep.

The amount of time spent in active sleep may be lower for animals subject to high risks of predation because arousal thresholds to external stimuli are higher during active sleep (Allison & van Wyver 1970a). Two studies that assessed the risk of predation by means of a subjective index found significant negative correlations between high predation risk and time spent in active sleep (Allison & Cicchetti 1976; Meddis 1983). However, the validity of this measure is unknown. Alternatively, a species' risk of predation may be indicated by its developmental status at birth. Altricial species are born less mature than precocial species, which are relatively well developed and independent at birth (Eisenberg 1981). Precocial species have also achieved more of their brain development at birth than altricial species (Martin 1981; Bennett & Harvey 1985). Zepelin (1980) and Meddis (1983), both using a crude measure of neonatal brain advancement at birth, found that relatively precocial species had less active sleep as adults than their altricial counterparts. Precocial species are generally larger than altricial species, however, so this relationship may also have been influenced by size.

In addition to the questions raised above, the comparative research on sleep suffers from several methodological problems. All studies have used species as the unit of statistical analysis. But species can seldom be treated as independent points in comparative analyses (Ridley 1983). Species within taxa may share suites of characters through common ancestry rather than convergent or parallel evolution. A relationship between two variables may have arisen in one ancestral species and not in another. If all descendants share their ancestral pattern, a statistical analysis of the species points can yield a significant but spurious relationship (see Elgar & Harvey 1987; Pagel & Harvey, in press).

Comparative studies can also be plagued by the effects of confounding variables (Clutton-Brock & Harvey 1984; Pagel & Harvey, in press). For example, Meddis (1983) has disputed the significance of the negative correlation between total sleep time and body weight reported by Zepelin & Rechtschaffen (1974) and Allison & Cicchetti (1976). Instead, Meddis (1983) claimed that the correlation is strongly influenced by the shorter sleeping times of grazing animals. Grazing mammals are also typically large. When Meddis (1983) removed grazing animals from his analysis the correlation between total sleep time and body

weight became non-significant (but see Zepelin's comment in Meddis 1983, page 93). Meddis (1983) argued that the correlations in the whole sample reflect the fact that because large grazing animals live in exposed habitats, they risk increased predation during sleep and therefore reduce their sleeping times.

In this paper we explore the relationships of sleep parameters with body weight, brain weight, patterns of development and metabolic rate, while controlling for confounding variables and possible taxonomic artefacts.

METHODS

Data Collection

We extracted from the literature sleep timings measured by EEG recordings, adult and neonatal brain and body weights, and basal metabolic rates (measured as cm^3 of oxygen consumption per h) for 69 species of mammals belonging to 12 orders (Table I). We followed Corbet & Hill's (1980) taxonomy, except that the Tupaiidae have been included within the Insectivora. Our sleep variables include total sleep time, quiet sleep time and active sleep time, each recorded as total time per 24 h, active sleep as a percentage of total sleep time (% active sleep), the duration of active sleep episode, and AS-QS cycle length (the time between the onset of successive active sleep episodes). We have included only sleep data that were collected from EEG recordings. Data for the echidna, *Tachyglossus aculeatus* (Allison et al. 1972) and two cetaceans *Tursiops truncatus* and *Phocoena phocoena* (Mukhametov et al. 1977; Mukhametov 1984) were excluded from the sample because they do not exhibit typical active sleep.

Each species was assigned to one of three geographical ranges (temperate, sub-tropical, tropical). Species were defined as temperate if they range exclusively outside the tropical zones, sub-tropical if their range overlaps temperate and tropical, and tropical if their range is exclusively within the tropics. Species were also assigned a dietary category. Geographical ranges and diets were from Walker (1983) and Macdonald (1985). Species were assigned to precocial and altricial

categories according to the age at eye opening of neonates (Case 1978). Species were classified as precocial if their neonates' eyes open at birth, and altricial otherwise.

Data Analysis

The distributions of body and brain weight, metabolic rate, active sleep time, AS-QS cycle length, and the duration of active sleep episodes were highly skewed and so were logarithmically transformed in order to make them more normal. The measures of total sleep time, quiet sleep time and % active sleep were more symmetrically distributed and were not transformed.

We employed nested analyses of variance (Sokal & Rohlf 1981) to determine an appropriate taxonomic level for analysis (see Harvey & Mace 1982; Pagel & Harvey, in press). In many comparative studies, species within families are very similar to each other and most variance in the data is concentrated among orders and families. Using genera or species as the level of analysis may increase the sample size, but does not add substantial new variance that is independent of taxonomic association. Conversely, analysis at higher taxonomic levels (e.g. order or above) may ignore appreciable amounts of variation at lower levels and unnecessarily reduce the sample size. The distribution of variance at successive taxonomic levels is given for each sleep variable in Table II. The highest proportion of variance was generally located among orders within the class, although considerable additional variance was also found among families within the orders. Species within genera and genera within families varied relatively little in these measures. We therefore chose the family as our unit of analysis.

Genus means were calculated from constituent species values, and family means were calculated from the constituent generic means. This procedure was complicated by missing data at the species level. Therefore, when calculating the genus means we excluded those species with incomplete data. Taxa were assigned the most representative category of geographical range and diet. There was very little variation within families in either variable.

Pearson correlation coefficients were used to assess the strength of relationships among vari-

Table 1. Sleep, constitutional and life history variables for 69 species of mammals from 12 orders

Taxon	Diet*	Geographical region†	Birth state‡	Adult body weight (g)	Adult brain weight (g)	Neonate brain weight (g)	BMR (cm ³ O ₂ per h)	Quiet sleep time (h)	Active sleep time (h)	AS-QS cycle (min)	Source of sleep data
Marsupialia											
Didelphidae											
<i>Didelphis marsupialis</i>	Omni	Tropic	Alt	3500.0	3.9	—	607.5	12.38	5.60	22.5	van Twyver & Allison (1970); Snyder et al. (1972)
<i>Latrodolus crassicaudata</i>	Verts	S/Tropic	Alt	1350.0	5.1	—	—	12.79	6.60	—	Afiani (1972)
Phalangeridae											
<i>Trichosurus vulpecula</i>	Leaves	S/Tropic	Alt	1982.0	11.4	—	634.2	11.90	1.80	—	LoPresti & McGinty (1970)
Macropodidae											
<i>Potorous tridactylus</i>	Grass	Temp	Alt	1600.0	—	—	—	10.06	0.60	—	Asie et al. (1979)
Edentata											
Bradypodidae											
<i>Bradypus tridactylus</i>	Leaves	Tropic	Pre	4250.0	15.3	—	682.2	8.93	1.58	38.0	de Moura Filho et al. (1983)
Dasyopodidae											
<i>Dasyops novemcinctus</i>	Inverts	S/Tropic	Pre	4600.0	8.4	3.5	796.8	14.27	3.13	22.8	van Twyver & Allison (1974)
<i>Prionomys maximus</i>	Inverts	Tropic	Pre	45190.0	81.0	—	3163.3	12.03	6.09	—	Afiani (1972)
Insectivora											
Tenrecidae											
<i>Tenrec ecaudatus</i>	Inverts	Tropic	Alt	790.0	2.6	—	260.7	13.26	2.34	—	Snyder et al. (1972)
Ermacidae											
<i>Ermacus europaeus</i>	Inverts	Temp	Alt	910.0	3.5	0.3	426.7	7.92	2.88	17.0	Snyder et al. (1972); Toutain & Ruckebusch (1975)
<i>Paracichnus hypomelas</i>	Inverts	Temp	Alt	550.0	2.4	—	112.5	7.50	2.82	—	Tauber et al. (1968)
Soricidae											
<i>Blarina brevicauda</i>	Inverts	Temp	Alt	21.0	0.3	—	52.5	12.19	2.71	7.6	Allison et al. (1977)
<i>Cryptotis parva</i>	Inverts	S/Tropic	Alt	5.0	0.1	—	—	7.70	1.40	8.8	Allison et al. (1977)
<i>Suncus murinus</i>	Inverts	S/Tropic	Alt	48.0	0.3	—	—	10.42	2.37	11.0	Allison et al. (1977)
Talpidae											
<i>Condylura cristata</i>	Inverts	Temp	Alt	70.0	1.0	—	—	8.15	2.17	7.4	Allison & van Twyver (1970b)
<i>Scalopus aquaticus</i>	Inverts	Temp	Alt	90.0	1.2	—	—	6.34	2.11	10.4	Allison & van Twyver (1970b)
Tupaiidae											
<i>Tupaia glis</i>	Inverts	S/Tropic	Alt	144.0	3.2	0.5	167.4	13.15	2.69	13.9	Berger & Walker (1972)
Chiroptera											
Vespertilionidae											
<i>Vespertilio fuscus</i>	Inverts	Temp	Pre	23.0	0.3	—	—	15.80	3.90	7.5	Zepelin & Rechtschaffen (1974)
<i>Myotis lucifugus</i>	Inverts	Temp	Pre	10.0	0.3	—	—	17.93	1.99	12.0	Brebbia & Pyne (1972)
Primates											
Lemuridae											
<i>Lemur macaco</i>	Leaves	Tropic	Pre	2500.0	25.6	—	—	9.31	0.34	—	Balzamo et al. (1978)
<i>Lemur mongoz</i>	Leaves	Tropic	Pre	1800.0	21.6	—	—	11.52	0.36	—	Balzamo et al. (1978)
Lorisidae											
<i>Galago senegalensis</i>	Fruit	Tropic	Pre	212.0	4.8	2.3	—	6.93	0.87	33.0	Bert et al. (1967)
Cebidae											
<i>Aotus tririgatus</i>	Fruit	Tropic	Pre	733.0	17.2	10.1	445.9	15.15	1.82	—	Perachio (1971)
<i>Saimiri sciureus</i>	Fruit	Tropic	Pre	752.0	22.4	15.3	489.7	7.14	2.75	—	Adams & Barratt (1974)
Cercopitheidae											
<i>Cercopithecus aethiops</i>	Fruit	Tropic	Pre	4173.0	64.2	48.0	—	9.74	0.60	—	Bert & Pagram (1969)
<i>Erythrocebus patas</i>	Fruit	Tropic	Pre	5600.0	106.6	—	—	9.99	0.86	—	Bert & Pagram (1969)
<i>Macaca mulatta</i>	Fruit	S/Tropic	Pre	5910.0	87.3	54.5	1990.6	11.05	0.71	44.5	Crowley et al. (1972); Meddis (1983)
<i>Macaca nemestrina</i>	Fruit	Tropic	Pre	7800.0	114.0	66.0	—	8.54	1.06	—	Kelle et al. (1965)
<i>Macaca radiata</i>	Fruit	Tropic	Pre	3700.0	76.8	—	—	8.12	1.05	—	Bert et al. (1972)
<i>Papio anubis</i>	Omni	Tropic	Pre	9500.0	175.1	—	2850.0	8.38	1.39	—	Balzamo & Bert (1975)
<i>Papio cynocephalus</i>	Omni	Tropic	Pre	16630.0	169.1	73.5	—	9.11	0.78	—	Balzamo (1973)
<i>Papio hamadryas</i>	Omni	Tropic	Pre	14350.0	136.0	75.0	—	8.58	1.26	14.0	Bert (1973)
<i>Papio papio</i>	Omni	Tropic	Pre	17600.0	192.0	53.0	2554.3	8.44	0.54	15.9	Bert (1973); Bert et al. (1975)
Pongidae											
<i>Pan troglodytes</i>	Omni	Tropic	Pre	45900.0	410.3	146.0	9594.0	9.18	1.62	90.0	Balzamo et al. (1972); McNew et al. (1971)
Hominae											
<i>Homo sapiens</i>	Omni	S/Tropic	Pre	60000.0	1250.0	384.0	14700.0	6.04	1.88	95.8	Meddis (1983)

Table 1 (continued)

Taxon	Diet*	Geographical region†	Birth state‡	Adult body weight (g)	Adult brain weight (g)	Neonate brain weight (g)	BMR (cm ³ O ₂ per h)	Quiet sleep time (h)	Active sleep time (h)	AS-QS cycle (min)	Source of sleep data
Carnivora											
<i>Canis familiaris</i>	Verts	Temp	Alt	14 000.0	70.0	6.8	—	9.67	3.24	20.0	Copley et al. (1976)
<i>Vulpes vulpes</i>	Verts	Temp	Alt	5900.0	48.0	3.8	4950.0	6.62	3.17	20.7	Dallaire & Ruckebusch (1974b)
Viverridae											
<i>Genetta genetta</i>	Verts	S/Tropic	Alt	1900.0	14.0	—	—	4.83	1.27	—	Meddis (1983)
Felidae											
<i>Felis silvestris</i>	Verts	S/Tropic	Alt	3260.0	28.4	5.6	2314.6	9.50	3.40	20.0	Lucas & Sterman (1974)
Pinnipedia											
<i>Phocaena</i>	Verts	Temp	Pre	85 000.0	325.0	—	—	6.08	0.12	—	Ridgway et al. (1975)
<i>Halichoerus grypus</i>	Verts	Temp	Pre	86 000.0	—	—	—	3.07	0.41	—	Mukhametov et al. (1984)
Perissodactyla											
<i>Equus caballus</i>	Grass	Temp	Pre	348 370.0	534.0	368.0	65 000.0	2.49	0.87	15.5	Dallaire & Ruckebusch (1974a)
Tapiridae											
<i>Tapirus terrestris</i>	Grass	Tropic	Pre	250 000.0	250.0	131.0	—	5.24	1.0	54.0	Zepelin (1970)
Hyacodidae											
<i>Dendrohyrax validus</i>	Leaves	Tropic	Pre	2000.0	12.3	—	928.2	4.66	0.24	—	Snyder (1974)
<i>Heterohyrax brucei</i>	Leaves	Tropic	Pre	1660.0	12.0	—	713.8	5.24	0.45	—	Snyder (1974)
<i>Procavia capensis</i>	Leaves	S/Tropic	Pre	2985.0	20.5	7.8	1078.3	4.66	0.24	—	Snyder (1974)
Artiodactyla											
Suidae											
<i>Sus scrofa</i>	Omni	Temp	Pre	145 000.0	180.0	30.0	8250.0	6.15	1.77	—	Ruckebusch (1972)
Bovidae											
<i>Bos indicus</i>	Grass	Temp	Pre	395 000.0	460.0	199.0	46 240.0	3.20	0.74	16.0	Ruckebusch (1972)
<i>Capra aegagrus</i>	Grass	Temp	Pre	29 000.0	115.0	61.2	6840.0	4.69	0.71	19.2	Bell & Tablaasdi (1973)
<i>Ovis aries</i>	Grass	Temp	Pre	43 000.0	100.0	52.0	10 200.0	3.28	0.56	16.5	Ruckebusch (1972)
Rodentia											
Sciuridae											
<i>Marmota flaviventris</i>	Omni	Temp	Alt	5000.0	—	—	—	15.61	1.81	10.0	Miller & South (1981)
<i>Spermophilus bellingeri</i>	Omni	Temp	Alt	300.0	—	—	—	12.83	3.11	12.5	Walker et al. (1977)
<i>Spermophilus lateralis</i>	Omni	Temp	Alt	720.0	3.0	—	—	12.02	3.86	8.3	Walker et al. (1977); Haskell et al. (1979)
<i>Spermophilus parryi</i>	Omni	Temp	Alt	980.0	5.7	—	—	12.70	3.38	—	Chepkasov (1980)
<i>Spermophilus tridecemlineatus</i>	Omni	Temp	Alt	861.0	4	—	—	10.39	3.41	—	van Twyver (1969)
Heteromyidae											
<i>Dipodomys deserti</i>	Nuts	Temp	Alt	60.0	—	—	—	13.28	2.72	7.3	Sakaguchi et al. (1979)
<i>Perognathus longimembris</i>	Nuts	Temp	Alt	8.2	—	—	16.4	16.91	3.15	9.0	Walker et al. (1983)
Muridae											
<i>Cricetomys gambianus</i>	Omni	Tropic	Alt	1000.0	6.6	—	—	6.30	2.00	—	Meddis (1983)
<i>Microstomys torquatus</i>	Leaves	Temp	Alt	70.0	8.9	—	92.6	12.00	3.19	8.6	Karmanova et al. (1979)
<i>Meriones angustidatus</i>	Omni	Temp	Alt	60.0	1.0	—	98.0	13.41	1.68	18.6	Kasimovs & Kaplan (1976)
<i>Mesocricetus auratus</i>	Omni	Temp	Alt	107.0	1.1	0.60	147.0	11.03	3.37	11.6	van Twyver (1969)
<i>Mus musculus</i>	Nuts	Temp	Alt	20.5	0.4	0.09	69.7	9.36	1.92	12.3	Friedman et al. (1975); Richardson et al. (1985)
<i>Rattus norvegicus</i>	Omni	Temp	Alt	265.0	3.3	0.28	312.8	10.67	2.58	8.5	van Twyver (1969)
<i>Sigmodon hispidus</i>	Grass	S/Tropic	Alt	132.0	1.2	0.31	145.2	9.82	1.48	14.5	Kilbuff & Ruckebusch (1976)
<i>Syllix leucodon</i>	Omni	Temp	Alt	208.0	3.0	—	160.16	8.22	2.39	—	Kardac (1967)
Citellidae											
<i>Geopocellus</i>	Grass	Temp	Pre	406.0	4.9	2.20	399.0	7.96	0.42	12.1	Jouvet-Mounier & Astic (1966)
Chinchillidae											
<i>Chinchilla laniger</i>	Grass	Temp	Pre	525.0	5.2	2.00	282.1	10.98	1.55	6.5	van Twyver (1969)
Apodidae											
<i>Apodemus rufa</i>	Grass	Temp	Pre	806.0	8.1	—	—	11.95	2.45	—	Snyder et al. (1972)
Ondatrae											
<i>Ondatra degus</i>	Omni	Temp	Pre	225.0	—	—	—	6.38	0.52	—	Mendelson (1982)
Lagomorphia											
Leporidae											
<i>Oryctolagus cuniculus</i>	Grass	S/Tropic	Alt	1600.0	11.1	1.2	—	7.34	1.37	29.0	Spies et al. (1970)

Sleep variables are given as units per 24 h. Data for body weight and metabolic rates are from Elgar & Harvey (1987) and Hayssen & Lacy (1985); adult and neonatal brain weight and state of development at birth are from Martin & Harvey (1985); diet and geographical range are from Macdonald (1985) and Walker (1983).

* Dietary classification: Omni: omnivorous; Verts: vertebrates; Inverts: invertebrates. Grazing animals are those feeding on grass or leaves.

† Geographical regions: Tropic: tropical; S/Tropic: sub-tropical; Temp: temperate; ‡ Birth state: Pre: precocial; Alt: altricial.

Table II. Distribution of variance at different taxonomic levels in sleep and life-history variables

Taxonomic level		Sleep and life-history variables								
		Adult body weight	Adult brain weight	Neonatal brain weight	Metabolic rate	Total sleep time	Quiet sleep time	Active sleep time	% Active sleep	AS-QS cycle
Among	Within									
Orders	Mammals	70.30	73.17	71.46	71.94	61.17	60.31	42.94	17.14	48.38
Families	Orders	17.09	17.19	23.06	18.96	23.03	15.72	43.00	55.34	30.54
Genera	Families	9.02	8.89	4.98	8.96	11.73	17.81	3.71	0.14	11.38
Species	Genera	3.59	0.75	0.50	0.14	4.07	6.16	10.35	27.38	9.70

The percentage variance refers to the additional variance located at that taxonomic level. The method used is described in Sokal & Rohlf (1981). AS: active sleep; QS: quiet sleep.

ables. Partial correlation was used to examine the relationship between pairs of variables, holding constant the effects of a third.

RESULTS

Characteristics of the Sample

Table III displays the mean values of the sleep variables for each order. Across families quiet sleep time made up 83% of total sleep time, ranging from 66% in the little water opossum, *Lutreolina crassicaudata* to 98% in the grey seal, *Halichoerus grypus*. Active sleep time ranged from 6.6 h down to 7 min in these same two species, respectively.

Sleep and Metabolism

Total and quiet sleep times were strongly negatively correlated with adult body weight, but the correlation of active sleep time with body weight was not significant (Table IV). Meddis (1983) found no relationship between quiet sleep time and body weight after removing large grazing mammals from his sample. However, in our sample, body weight was significantly negatively correlated with total and quiet sleep times both across the 12 grazing families (i.e. those that feed on grass and leaves, see Table I; total sleep time: $r = -0.731$, $P < 0.01$; quiet sleep time: $r = -0.783$, $P < 0.01$) and across the 22 non-grazing families (total sleep time: $r = -0.459$, $P < 0.05$; quiet sleep time: $r = -0.483$, $P < 0.03$). The difference between our results and those of Meddis is probably due to the classification of grazing animals. Whereas Meddis included primarily the artiodactyls, our data included a wider taxonomic range of grazers (see Table I).

It has been argued that smaller animals, with their higher mass-specific metabolic rates (i.e. $O_2/g/h$), have evolved longer daily sleeping times in response to selection to conserve energy. If that explanation is correct, animals of the same size with higher metabolic rates should also sleep for longer. A direct test of whether metabolic rate is related to sleep independently of size can be made by partial correlation. We correlated total and quiet sleep times with metabolic rate, after removing the effects of adult body weight. In both instances the partial correlations were significant and negative (total sleep time: partial $r = -0.402$, $P < 0.05$, $N = 26$; quiet sleep time: $r = -0.457$, $P < 0.05$, $N = 26$). Thus increasing metabolic rate for a given body weight (i.e. increasing the mass-specific metabolic rate) is associated with less sleep (Fig. 1). This result contradicts the view that the variation in sleep duration is due to energy conservation (Zeppelin & Rechtschaffen 1974; Berger 1975; Allison & Cicchetti 1976; Walker & Berger 1980), but is consistent with the idea that the amount of feeding and foraging time needed to meet metabolic needs limits the time available for sleep.

Active Sleep and Thermoregulation

Mammals most vulnerable to excessive drops in body temperature may have less active sleep time or shorter active sleep episodes because mechanisms of thermoregulation are generally thought to be less effective during active sleep. Such species may include those with high metabolic rates for their body sizes, those with smaller bodies (whose high surface to volume ratios increase their vulnerability to heat loss), and those living in temperate rather than tropical regions.

Table III. Mean values of sleep variables within mammalian orders

Order	Total sleep (h)	Quiet sleep (h)	Active sleep (h)	% Active sleep	AS-QS cycle (min)
Artiodactyla	5.28 (1.9) 4	4.33 (1.4) 4	0.94 (0.6) 4	17.30 (4.2) 4	17.2 (1.7) 3
Carnivora	10.42 (3.2) 4	7.66 (2.3) 4	2.77 (1.0) 4	25.58 (4.9) 4	20.23 (0.4) 3
Chiroptera	19.80 (2) 2	16.87 (1.5) 2	2.95 (1.4) 2	14.90 (6.9) 2	9.75 (3.2) 2
Edentata	15.34 (4.2) 3	11.74 (2.7) 3	3.60 (2.3) 3	22.20 (10.0) 3	30.40 (10.7) 2
Hyracoidea	5.16 (0.5) 3	4.85 (0.3) 3	0.31 (0.1) 3	5.83 (1.8) 3	— — —
Insectivora	12.01 (2.8) 9	9.63 (2.7) 9	2.39 (0.5) 9	20.99 (4.9) 9	10.87 (3.5) 7
Lagomorpha	8.71 — 1	7.34 — 1	1.37 — 1	15.70 — 1	29.00 — 1
Marsupialia	15.43 (4.0) 4	11.78 (1.2) 4	3.65 (2.9) 4	20.75 (13.8) 4	22.50 — 1
Perissodactyla	4.80 (2.0) 2	3.87 (1.9) 2	0.93 (0.1) 2	21.00 (7.1) 2	34.75 (27.2) 2
Pinnipedia	4.76 (1.9) 2	4.50 (2.1) 2	0.26 (0.2) 2	12.55 (1.2) 2	— — —
Primates	10.32 (2.1) 16	9.20 (2.1) 16	1.12 (0.6) 16	11.12 (6.8) 16	48.87 (35.9) 6
Rodentia	13.47 (3.3) 19	11.16 (2.8) 19	2.31 (0.9) 19	16.87 (5.7) 19	10.75 (3.3) 13

Standard deviations are given in parentheses, with number of species below. AS: active sleep; QS: quiet sleep.

Total active sleep time had weak, negative correlations with adult body weight and basal metabolic rate (Table IV) which became weaker when active sleep was expressed as a percentage of total sleep time (Table IV).

There are too few data points for duration of active sleep episodes to allow sensitive analyses at the family level, but there was a significant correlation at the species level between duration of active sleep episodes and AS-QS cycle length ($r=0.74$,

$P<0.001$, $N=25$), indicating that the length of time between successive active sleep episodes (i.e. the AS-QS cycle) declines as the active sleep episodes become shorter. We have therefore used AS-QS cycle length as a surrogate variable for duration of active sleep episodes in the family-level analyses.

AS-QS cycle length had very strong positive correlations with both adult body weight and basal metabolic rate (Table IV). Thus, smaller animals have shorter active sleep episodes (as measured by AS-QS cycle length), a result that replicates Zeppelin & Rechtschaffen (1974) and Meddis (1983). The correlation of AS-QS cycle length with basal metabolic rate may be due to the greater rate of heat loss per unit of body weight in smaller animals. But what about mammals with relatively high metabolic rates for their size? The correlation of AS-QS cycle with metabolic rate was not significant after controlling for the effects of body size. Thus, mammals with high energy expenditure for their size do not have shorter active sleep episodes.

Nevertheless, if thermoregulation is inefficient during active sleep, mammals in cold geographical regions may have shorter AS-QS cycles than would be expected for their body size. We found a significant association between AS-QS cycle length and geographical region after controlling for the effects of body weight with analysis of covariance ($F=6.99$, $P<0.01$, $N=23$): most of the effect for geographical region was due to tropical families having relatively longer cycles than temperate families (Fig. 2). The implication is that mammals in colder geographical regions reduce their active sleep episode duration in order to maintain thermoregulation. This pattern cannot be entirely separated from taxonomy, but there is variation within five of six orders according to geographical region that supports the idea. The exception is within the primates, where humans have exceptionally long AS-QS cycles.

Active Sleep in Precocial and Altricial Species

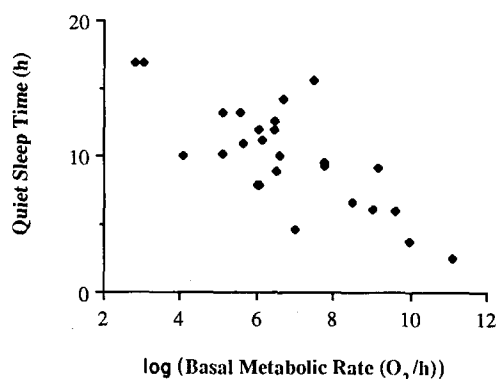
Altricial families had significantly longer active sleep time than precocial families (mean altricial=2.48 h, mean precocial=1.33 h, $t=3.10$, $P<0.01$, $N=34$). Since altricial and precocial families also differed in average body size, we controlled for body weight with analysis of covariance, and the difference remained significant: precocial families had less active sleep time, indepen-

Table IV. Correlations between sleep variables and logarithmically transformed adult brain and body weights, and metabolic rates across families of mammals

Sleep variables	Adult body weight	Adult brain weight	Basal metabolic rate (O_2 h)
Total sleep time (h)	-0.569** (34)	-0.588** (29)	-0.715** (26)
Quiet sleep time (h)	-0.595** (34)	-0.604** (29)	-0.752** (26)
Active sleep time (h)	-0.296* (34)	-0.342* (29)	-0.318* (26)
% Active sleep	0.145 (34)	0.078 (29)	-0.246 (26)
AS-QS cycle length (min)	0.637** (22)	0.723** (20)	0.592** (26)

The number of families is given in parentheses. AS: active sleep; QS: quiet sleep.

* $P < 0.1$ (two-tailed); ** $P < 0.01$ (two-tailed).

**Figure 1.** The amount of time spent in quiet sleep during a 24-h period versus basal metabolic rate ($cm^3 O_2$ per h).

dent of body size, than altricial families ($F=6.87$, $P < 0.01$, $N=19$). Active sleep also occupied a significantly lower percentage of total sleep time in precocial families than in altricial families, independent of body size ($F=8.22$, $P < 0.01$, $N=19$). Many precocial species, being large, rear their young above ground rather than in burrows (Eisenberg 1981). Perhaps the increased risk of predation during sleep to young reared this way has led to less active sleep. However, there was no tendency for precocial families to have shorter active sleep episodes than altricial families, after controlling for body size.

AS-QS Cycle Length and Brain Weight

Zepelin & Rechtschaffen (1974) and Meddis (1983) found a strong relationship between brain weight and the AS-QS cycle length, independent of its association with body weight or metabolic rate.

We conducted a multiple regression to predict AS-QS cycle length from adult body weight, basal metabolic rate and adult brain weight. After controlling simultaneously for adult body size and metabolic rate, adult brain weight was still significantly related to cycle length (partial $r=0.663$, $F=9.42$, $P < 0.01$, $N=20$); animals with larger relative brain sizes have longer AS-QS cycle lengths. Metabolic rate was not significantly related to AS-QS cycle length after controlling for body size. However, this result seems to depend on humans, who have very large brains for their body weight. When humans were removed from the analysis, brain weight no longer correlated with cycle length independently of adult body weight or of metabolic rate.

DISCUSSION

Several authors have argued that it is difficult to interpret the results of comparative analyses of sleep because of the unreliability of the data (Campbell & Tobler 1984; McFarland 1988). Data on sleep parameters have been obtained primarily from laboratory studies, where the animals are not under natural conditions and may not show typical sleep patterns. Furthermore, these laboratory studies have failed to standardize those variables that affect sleep, for example, age, light/dark schedules, nutritional requirements and ambient temperature, or even the 'quality' of sleep (Campbell & Tobler 1984). In spite of this, our analysis of the comparative sleep data has shown consistent patterns of associations between sleep variables and aspects of species' morphology, metabolic rate and development. Moreover, quiet sleep was correlated with a different set of variables from those

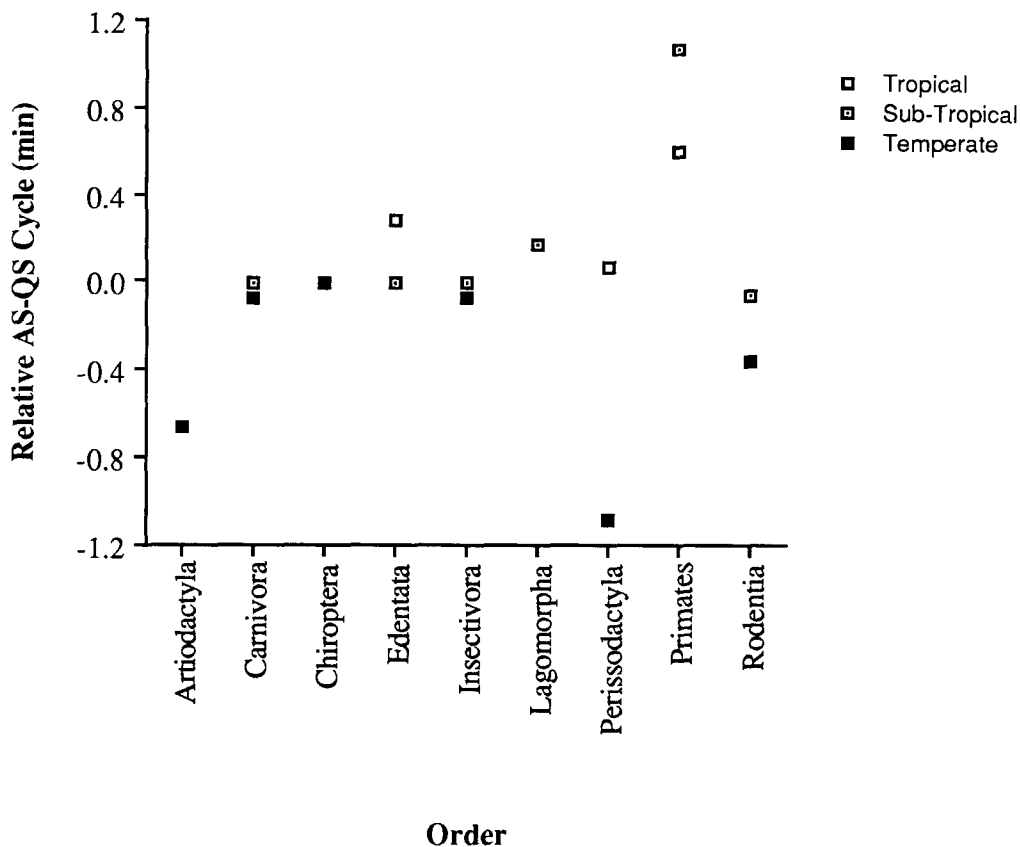


Figure 2. Length of the active-sleep–quiet-sleep (AS–QS) cycle adjusted for body size in relation to geographical region. Points represent averages of families within the order. The AS–QS cycle is described in the Methods.

associated with active sleep. Time spent in quiet sleep was negatively correlated with body weight and basal metabolic rate, whereas the percentage of time spent in active sleep was lower for precocial than for altricial species. These correlations would presumably be improved if the data set were drawn from studies that employed standardized experimental techniques.

Since energy expenditure is reduced during sleep, it has been proposed that sleep duration has evolved to balance metabolic costs. This idea is supported by comparative studies showing that smaller mammals, with higher mass-specific metabolic rates, sleep more than larger mammals (Zeppelin & Rechtschaffen 1974; Berger 1975; Allison & Cicchetti 1976; Walker & Berger 1980). An alternative explanation is that the negative relationship between body size and sleep would arise if larger mammals need to spend a greater proportion of

their day foraging in order to meet their greater metabolic needs. For example, Clutton-Brock & Harvey (1977) report a positive relationship between body size and the time spent foraging in primates. Our analyses of metabolic rate and sleep time, controlling for body size, allow us to distinguish between these two explanations. Metabolic rate was negatively correlated with sleep time, after removing the effects of body size. Thus, higher metabolic rates are associated with less sleep, independently of body size. We suggest that the duration of quiet sleep may reflect foraging requirements rather than the need to conserve energy (although this idea requires further investigation).

The duration of active sleep episodes, estimated by the AS–QS cycle length, was positively correlated with body weight and metabolic rate, and significantly associated with geographical locality. Perhaps this indicates the influence of reduced

thermoregulatory effectiveness during active sleep? Smaller animals had shorter active sleep episodes than larger animals, and animals living in colder climates had shorter active sleep episodes, for their sizes, than those living in more temperate climates. Perhaps the reduced heat loss brought about by the tendency for small mammals to sleep in insulating nests or burrows, or huddled together is not enough to alter substantially the relationships among active sleep, metabolic rate and body weight. The pattern we observed for active sleep might reduce the extent of drops in body temperature, while maintaining total active sleep time. In fact, active sleep in ground squirrels, *Citellus* spp., almost disappears during hibernation (Walker et al. 1977). Experiments with laboratory rats show that active sleep increases with higher temperatures, although it decreases sharply at 31°C and is almost non-existent at higher temperatures (Szymusiak & Satinoff 1981). Furthermore, rats in quiet sleep at temperatures below the thermoneutral zone are more likely to enter active sleep if the skin temperature is raised (Szymusiak et al. 1980). Hamsters, *Mesocricetus auratus*, also reduce the amount of time in active sleep at lower ambient temperatures, although without changes in the duration of active sleep episodes (Sichieri & Schmidek 1984). Species may not be able to alter the duration of active sleep episodes facultatively.

The relationships between body size, geographical region and AS-QS cycle might also be interpreted in terms of starvation risks. The gut volume of mammals varies in direct proportion to body size (Calder 1984) and smaller mammals with their higher mass-specific metabolic rate may therefore need to feed more often to avoid starvation (Harvey 1985). If the AS-QS cycle is positively correlated with the overall sleep cycle (i.e. the time from the onset of sleep to the next period of wakefulness), then the positive correlation between body weight and AS-QS cycle may arise because smaller mammals intersperse periods of sleep with periods of foraging more frequently than larger mammals. Furthermore, for any given body weight, animals in colder climates may experience a greater risk of starvation, and hence need to forage more frequently. This interpretation of AS-QS cycle times in terms of starvation risk may also explain why we found no relationship between AS-QS cycle and metabolic rate after controlling for size. Animals with high metabolic rates for their size may need to feed more often only if they are

small and thus have small gut volumes. The relationships among body weight, AS-QS cycle and geographical region clearly merit further investigation.

Active sleep time was strongly correlated with whether a species is precocial or altricial, despite being unrelated to measures of size or metabolic rate. Adults of precocial species had much less total active sleep than adults of altricial species even after controlling for the size difference between these two groups. This relationship may be a consequence of precocial species having more fully developed brains at birth than altricial species, since active sleep usually predominates in the developing brain (Roffwarg et al. 1966; Meddis 1983). This explanation implies that patterns of active sleep are set at birth, or at least that differences between the species at birth are related to their active sleep patterns as adults. If having precocial offspring is an adaptation to avoid predation (e.g. Eisenberg 1981), less active sleep throughout life might be expected in precocial species. This interpretation remains doubtful, however, since there was no tendency for precocial families to have shorter active sleep episodes than altricial families.

Zepelin & Rechtschaffen (1974) found that adult brain weight is related to the length of the AS-QS cycles, independently of body size. The combined effects of body size and brain size on AS-QS cycle length were that large animals, and animals with large brains for their body sizes, have longer AS-QS cycles, and, by inference, longer active sleep episodes. However, our analysis shows that this relationship is probably an artefact of including data on humans in the analyses. The significant correlation disappeared when humans, who have both very large brains for their body size and also long cycles, were removed. The relationships of sleep variables with brain size (Allison & Cicchetti 1976; Meddis 1983) are probably due to the strong association of brain size with body size.

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