

Mammalian Sleep, Longevity, and Energy Metabolism¹

HAROLD ZEPELIN and ALLAN RECHTSCHAFFEN

Oakland University, Rochester, Mich. and University of Chicago, Chicago, Ill.

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Abstract. Based on data for 53 mammalian species reported in the literature, statistical analyses revealed that daily sleep quotas correlate positively with metabolic rate and negatively with maximum life span and brain weight. Sleep cycle length correlates positively with life span and brain weight and negatively with metabolic rate. Paradoxical sleep figures in these intercorrelations only by virtue of its positive correlation with slow wave sleep. The correlation between sleep time and metabolic rate suggests that sleep has the function of enforcing rest and limiting metabolic requirements, although some inconsistent findings are noted. Strong correlations of cycle length with brain weight and metabolic rate suggest that the significance of cycle length has not been sufficiently explored.

Introduction

Discussions of the function of sleep contain speculations about a possible relationship between the life spans and daily sleep quotas of mammalian species [6, 8, 50, 121]. Such speculations derive from the theory that the function of sleep is to enforce rest and conserve energy [90, 143]. The potential or maximum life spans of mammalian species and their bas-

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al rates of energy metabolism per unit of body weight are inversely correlated [25, 110], suggesting that energy expenditure represents 'wear and tear' on the capacity for living. It therefore seems possible that sleep, by restricting energy expenditure, promotes longevity, and that long life spans are associated with high daily sleep quotas. Such reasoning has been fostered especially by the example of the bat, which can live about 20 years in spite of an extremely high metabolic rate. The contrast between the long life span of the bat and the short life spans of other species with similar metabolic rates (for example, the short-tailed shrew, which lives about 2 years) seems to be explained by the much greater length of the bat's daily sleep and by the sharp drop in metabolic rate during its sleep period [6, 81].

If sleep serves to restrict energy expenditure, daily sleep quotas should be significantly correlated with longevity and metabolic rate. The present study was conducted to assess these possibilities with respect to mammalian species. It was based on a review of the data that have accumulated in many different laboratories during the past two decades as a result of intensified scientific interest in both sleep and longevity. The study was confined to mammals because information on sleep in other classes is still meager.

It was apparent from the outset of this study that the available data would be less than ideal. Most estimates of daily sleep quotas have come from electroencephalographic (EEG) studies of animals caged in laboratories, and it is not yet known how accurately the findings of such studies reflect the sleep patterns of animals in their natural habitats. Some estimates of sleep quotas have been obtained by visual observations of confined animals in zoos, stables, or enclosures, a method whose reliability and generalizability also are questionable. Similar problems affect the data on longevity. Perhaps the most meaningful measure of longevity is life expectancy (average survival time), but the data based on this measure are available for very few species. Consequently, potential or maximum life span is presently the most useful measure for comparative purposes. This measure can be criticized on two grounds: it depends largely on zoo records, whose reliability may be questioned [40], and since it represents the hardest members of a species, it is likely to increase as sample size increases.

These limitations of the data notwithstanding, a comparison of sleep quotas and maximum life spans is appropriate and timely. Coarseness of measurement alone cannot explain the wide interspecies differences in

sleep quotas which greatly exceed intraspecies variation [6, 121]. SACHER [110] has persuasively defended maximum life span as the parameter of longevity that is least dependent on environmental influences and is therefore most appropriate as a measure of the intrinsic capacity for life. Moreover, SACHER's finding [110, 111] that maximum life span correlates positively with brain weight and negatively with metabolic rate has demonstrated its significance as a biophysical dimension. It is apparent that the conclusions based on the presently available data on sleep and longevity must be somewhat tentative, but there is no sound reason to disregard these data, especially since the function of sleep must still be described as an enigma [121]. To forego analysis of these data because of their shortcomings could mean the unnecessary postponement of insights that are within reach.

Method

Data Selection

Table I summarizes the principal data on daily sleep quotas and other sleep parameters in 53 species representing 12 orders and 33 families. The tree shrew has been listed as a primate, but because of persistent controversy about its classification as a primate or as an insectivore [142] it was not included in either order in analyses that were limited to orders.

Because paradoxical sleep (PS) and slow wave sleep (SWS) are often assumed to have distinct functions, the daily quotas of PS and SWS and the proportion of PS to total sleep time (TST) were assessed independently, along with TST, in relation to life span and other constitutional variables. Distinctions between SWS and PS are outlined below. Values for SWS do not appear in table I but can be derived by subtracting PS time from TST. (Mean SWS time for 40 species listed in table I with the necessary data was 9.5 h; SD = 3.8.) The PS percentage = PS time/TST \times 100.

An additional sleep parameter listed in table I is the duration of the sleep cycle, which was included for study because the sleep of virtually all mammalian species is organized in cycles. A cycle consists of a period of SWS and the succeeding period of PS, the two periods together occupying a duration that is characteristic of a species. This duration may be described as the duration of sleep between the onset of one PS period and the next, or between the end of one PS period and the end of the next. In previous studies with data for small numbers of species, WEISS and ROLDAN [146] and HARTMANN [62] found that cycle length correlates negatively with metabolic rate per unit of body weight. Hence cycle length could be expected to correlate positively with life span.

Table II summarizes the principal data on life span and other constitutional variables whose relationships to sleep parameters were assessed. Basal or resting rates of oxygen consumption measured by calorimetric methods were available for some species, but to maximize the data, estimates of metabolic rates were derived from body weights which are shown in the table. This derivation was justified by the

Table 1. Sleep parameters in 53 mammalian species

Orders, families and species	TST, h	PS time, h	PS %	Sleep cycle, min
<i>Monotremata</i>				
<i>Tachyglossidae</i>				
Echidna	8.6	— ¹	— ¹	— ¹
<i>Marsupialia</i>				
<i>Didelphidae</i>				
North American opossum	18.0	4.9	27.0	19.7
Water opossum	19.4	6.6	33.7	—
<i>Phalangeridae</i>				
Phalanger	13.7	1.8	13.0	—
<i>Macropodidae</i>				
Red kangaroo	—	—	8.7	14.7
<i>Insectivora</i>				
<i>Tenrecidae</i>				
Tenrec	15.6	2.3	15.0	—
<i>Erinaceidae</i>				
European hedgehog	14.1	3.9	28.0	—
Desert hedgehog	10.3	2.7	26.0	—
<i>Talpidae</i>				
Eastern American mole	8.4	2.1	25.0	10.4
Star-nosed mole	10.3	2.2	21.7	—
<i>Chiroptera</i>				
<i>Vespertilionidae</i>				
Little brown bat	19.9	2.0	10.0	12.0
Big brown bat	19.7	3.9	20.0	7.5
<i>Primates</i>				
<i>Tupaiaidae</i>				
Tree shrew	15.8	2.6	16.8	13.9
<i>Lorisidae</i>				
Slow loris	11.0	—	—	—
Galago	10.7	1.2	11.2	33.0
<i>Cebidae</i>				
Owl monkey	17.0	1.8	10.6	—
<i>Cebinae</i>				
Squirrel monkey	9.9	—	—	—
<i>Cercopithecidae</i>				
Vervet	10.3	0.6	5.6	—
Patas monkey	10.9	0.9	7.9	—
Rhesus monkey	9.6	1.2	12.7	44.5
Baboon	9.8	0.7	7.2	40.0

Table 1 (continued)

Orders, families and species	TST, h	PS time, h	PS %	Sleep cycle, min
<i>Primates</i>				
<i>Pongidae</i>				
Chimpanzee	9.7	1.4	15.0	90.0
<i>Hominidae</i>				
Man	8.0	1.9	24.2	95.8
<i>Edentata</i>				
<i>Dasypodidae</i>				
Giant armadillo	18.1	6.1	33.7	—
Nine-banded armadillo	18.5	4.0	21.5	—
<i>Lagomorpha</i>				
<i>Leporidae</i>				
Rabbit	8.4	0.9	10.7	29.0
<i>Rodentia</i>				
<i>Aplodontiidae</i>				
Mountain beaver	14.4	2.4	17.0	—
<i>Sciuridae</i>				
Yellow-bellied marmot	—	—	20.0	—
Ground squirrel	13.8	3.4	24.7	12.5
Arctic ground squirrel	16.5	—	—	—
<i>Cricetidae</i>				
Golden hamster	14.4	3.3	22.9	11.6
<i>Spalacidae</i>				
Mole rat	10.6	2.4	22.5	—
<i>Muridae</i>				
Rat	13.6	2.5	18.6	9.8
Mouse	12.8	1.2	9.5	9.6
<i>Cavidae</i>				
Guinea pig	8.2	0.8	9.7	12.1
<i>Chinchillidae</i>				
Chinchilla	12.5	1.5	12.4	6.5
<i>Carnivora</i>				
<i>Canidae</i>				
Gray wolf	13.0	—	—	—
Red fox	9.8	2.4	24.5	20.7
Arctic fox	12.5	—	—	—
<i>Procyonidae</i>				
Raccoon	12.5	—	—	—
<i>Felidae</i>				
Cat	14.5	3.6	24.9	27.5
Jaguar	10.8	—	—	—

Table I (continued)

Orders, families and species	TST, h	PS time, h	PS %	Sleep cycle, min
<i>Proboscidea</i>				
<i>Elephantidae</i>				
Asian elephant	3.9	1.8	46.2	124.0
African elephant	3.3	—	—	—
<i>Perissodactyla</i>				
<i>Equidae</i>				
Horse	2.9	0.8	27.3	60.0
Donkey	3.1	—	—	—
<i>Tapiridae</i>				
Brazilian tapir	6.2	1.0	16.0	54.0
<i>Artiodactyla</i>				
<i>Cervidae</i>				
Roe deer	2.6	—	—	—
<i>Giraffidae</i>				
Giraffe	—	0.3	—	—
Okapi	—	1.0	—	—
<i>Bovidae</i>				
Goat	3.8	0.5	13.2	—
Sheep	3.8	0.6	14.7	—
Cow	3.9	0.7	18.9	40.0
N	49	40	40	24
Mean	11.2	2.1	18.7	33.3
SD	4.8	1.5	8.6	31.4
Mean log ²		0.228	1.226	1.364
SD log ²		0.315	0.206	0.371

Dashes indicate that no data were available.

¹ Not present in this species: species omitted from calculations for this variable.

² Log values are given only for transformed variables.

well-documented relationship between body weight and metabolic rate in mammals. KLEIBER [74] has reported a linear correlation of 0.98 between body weight and metabolic rate (kcal/animal/day) when both are expressed in logarithmic form, and he has demonstrated that the daily metabolic rate for a member of a species can be satisfactorily estimated as 70 times the three-fourths power of body weight (in kg). BRODY [31] reported similar findings. KLEIBER's [74] formula was used to calculate metabolic rates from body weights. To facilitate comparisons between estimated rates and rates determined by calorimetric methods, both measures were translated into weight-specific form, i.e., metabolic rates per unit body weight. (In this form,

Table II. Constitutional variables in 53 mammalian species

Orders, families and species	Life span years	O ₂ consumption cm ³ /g/h	Body weight kg	Brain weight g	Gestation period days
<i>Monotremata</i>					
<i>Tachyglossidae</i>					
Echidna	50.0	0.22	3.000	—	—
<i>Marsupialia</i>					
<i>Didelphidae</i>					
North American opossum	5.0	0.52	1.700	6.3	12
Water opossum	—	—	0.370	—	14
<i>Phalangeridae</i>					
Phalanger	13.0	—	1.620	11.4	17
<i>Macropodidae</i>					
Red kangaroo	16.3	—	35.000	—	33
<i>Insectivora</i>					
<i>Tenrecidae</i>					
Tenrec	—	—	2.000	—	—
<i>Erinaceidae</i>					
European hedgehog	6.0	0.75	0.785	3.5	42
Desert hedgehog	—	—	0.550	—	—
<i>Talpidae</i>					
Eastern American mole	3.5	1.90	0.040	1.2	42
Star-nosed mole	3.5	—	0.060	—	—
<i>Chiroptera</i>					
<i>Vespertilionidae</i>					
Little brown bat	20.5	2.00	0.010	—	50
Big brown bat	19.0	—	0.023	0.3	35
<i>Primates</i>					
<i>Tupaiaidae</i>					
Tree shrew	2.3	—	0.104	2.5	46
<i>Lorisidae</i>					
Slow loris	12.7	—	1.000	—	90
Galago	10.4	—	0.200	5.0	120
<i>Cebidae</i>					
Owl monkey	12.0	0.51	0.480	15.5	140
<i>Cebinae</i>					
Squirrel monkey	20.0	0.83	0.610	20.0	—
<i>Cercopithecidae</i>					
Vervet	24.0	—	4.190	58.0	210
Patas monkey	20.2	—	10.000	—	—
Rhesus monkey	29.0	0.43	6.786	118.4	164
Baboon	27.0	—	10.546	179.5	180

Table II (continued)

Orders, families and species	Life span years	O ₂ consumption cm ³ /g/h	Body weight kg	Brain weight g	Gestation period days
<i>Primates</i>					
<i>Pongidae</i>					
Chimpanzee	50.0	0.25	52.160	440.0	230
<i>Hominidae</i>					
Man	100.0	0.22	62.080	1,320.0	267
<i>Edentata</i>					
<i>Dasypodidae</i>					
Giant armadillo	—	—	50.000	—	—
Nine-banded armadillo	6.5	0.25	3.500	10.8	120
<i>Lagomorpha</i>					
<i>Leporidae</i>					
Rabbit	18.0	0.42	2.530	12.1	31
<i>Rodentia</i>					
<i>Aplodontiidae</i>					
Mountain beaver	—	—	1.350	—	45
<i>Sciuridae</i>					
Yellow-bellied marmot	13.0	—	4.050	17.0	38
Ground squirrel	9.0	0.87	0.101	4.0	28
Arctic ground squirrel	—	0.59	0.920	5.7	—
<i>Cricetidae</i>					
Golden hamster	3.9	0.93	0.120	1.0	16
<i>Spalacidae</i>					
Mole rat	—	0.77	0.122	3.0	30
<i>Muridae</i>					
Rat	4.7	0.86	0.280	1.9	21
Mouse	3.2	1.49	0.023	0.4	19
<i>Cavidae</i>					
Guinea pig	7.6	0.74	1.040	5.5	68
<i>Chinchillidae</i>					
Chinchilla	7.0	—	0.425	6.4	112
<i>Carnivora</i>					
<i>Canidae</i>					
Gray wolf	16.2	0.32	36.328	119.5	63
Red fox	9.8	0.52	4.235	50.4	52
Arctic fox	14.0	0.52	3.385	44.5	60
<i>Procyonidae</i>					
Raccoon	13.7	0.39	4.288	39.2	63

Table II (continued)

Orders, families and species	Life span years	O ₂ con- sumption cm ³ /g/h	Body weight kg	Brain weight g	Gestation period days
<i>Carnivora</i>					
<i>Felidae</i>					
Cat	28.0	0.44	3.303	25.6	63
Jaguar	22.4	—	100.000	—	100
<i>Proboscidea</i>					
<i>Elephantidae</i>					
Asian elephant	69.0	0.07	2,547.333	4,603.0	624
African elephant	38.6	—	6,654.000	5,712.0	645
<i>Perissodactyla</i>					
<i>Equidae</i>					
Horse	46.0	0.15	521.640	655.0	336
Donkey	40.0	—	187.072	419.0	365
<i>Tapiridae</i>					
Brazilian tapir	30.4	—	160.000	169.0	392
<i>Artiodactyla</i>					
<i>Cervidae</i>					
Roe deer	17.0	—	14.828	98.2	150
<i>Giraffidae</i>					
Giraffe	28.0	—	529.000	680.0	400
Okapi	15.1	—	250.000	—	440
<i>Bovidae</i>					
Goat	20.0	0.19	27.660	115.0	148
Sheep	20.0	0.24	55.500	175.0	151
Cow	30.0	0.13	465.000	423.0	281
n	47	29	53	40	45
Mean	20.9	0.6	223.1	389.4	145.6
SD	18.5	0.48	971.2	1,144.5	158
Mean log	1.175	-0.343	3.582 ¹	1.484	1.927
SD log	0.370	0.345	1.343 ¹	1.055	0.471

Dashes indicate that no data were available.

¹ Based on grams.

metabolic rate is inversely correlated with body weight, but the absolute value of the correlation is unchanged.) The use of the two measures of metabolic rate not only maximized the data but also permitted detection of departures from the predicted relationship between body weight and metabolic rate which are known to exist [31, 83, 118].

Brain weight was included for study because, despite a strong relationship between brain weight and body weight, there are species differences with respect to this relationship [141]. There is a positive correlation between brain weight and life span that is independent of the relationship between life span and body weight or metabolic rate [110, 111]. It therefore seemed possible that there are relationships between brain weight and sleep parameters which are independent of any relationships between sleep parameters and life span or metabolic rate. Such a possibility has been intimated in KLEITMAN's theory [75] that the amount of wakefulness per day is positively related to corticalization.

Length of gestation period was included for study because, on the basis of previous studies with data for small numbers of species [62, 146], a positive correlation between length of gestation period and the length of the sleep cycle could be expected. BOURLIERE [26] has also reported a positive correlation between life span and the length of gestation period.

The data on sleep were drawn from the literature on mammalian sleep-wakefulness patterns. Purely anecdotal reports on sleep quotas were disregarded. In a few instances, when several systematic studies were available for a single species, it seemed essential to make a choice of data on methodological grounds. These instances are described in more detail below. Otherwise, the results of systematic studies were incorporated without judgment as to their methodological merits. In a number of cases, as described below, the results of several studies were consolidated. It was recognized that the data for the different species were not uniformly reliable, but the setting of methodological standards for the inclusion of data might have frustrated the aims of the study since there are few species that have been studied as adequately as can be desired. It seemed most important to strive for comprehensiveness and for a broad sample of species. Comparability between the different studies in the scoring of sleep time could be assumed because there is consensus among investigators that the same behavioral and electrographic signs of sleep occur in all mammals. There is agreement that the occurrence of sleep can be judged behaviorally by sustained immobility in a recumbent posture with the eyes closed. The elevation of sensory thresholds is also an agreed-upon behavioral criterion of sleep, but in the presence of other sleep signs, a change in thresholds is usually assumed rather than demonstrated. There is agreement that the occurrence of SWS can be judged electrographically by the appearance of spindles and synchronized, high-amplitude, slow activity in the EEG, and that PS can be distinguished from the rest of sleep by a combination of (1) desynchronized, low-amplitude, relatively fast EEG activity without spindles or slow waves, (2) the occurrence of rapid eye movements, and (3) in most species, the abolition of tonus in the neck muscles. Other agreed-upon signs of PS are twitching of the facial muscles and of the extremities, respiratory irregularity, and in some species, the elevation of sensory thresholds beyond the level in SWS.

Despite the general consensus on the foregoing sleep criteria, it was necessary to take note of some problems in the definition and quantification of sleep that are yet to be resolved. There is controversy regarding the classification of drowsiness, a state which is associated with behavior that seems wakeful (e.g., an erect posture, opening and closing of the eyes, ruminating) and with the intermittent appearance

of slow components, spindles, or high-amplitude, slow waves against the background of a waking EEG [105, 106, 127, 136]. In some species, such as man or the rat, drowsiness is transitory and brief and therefore does not pose a significant problem in the calculation of daily sleep quotas. But in other species, such as the cat and the cow, drowsiness occupies several hours a day. Some investigators take the view that drowsiness should be counted as wakefulness, others argue that it should be counted as sleep, and still others contend that the significance of drowsiness and its classification depend on the species in question [5]. The approach taken in the present study was twofold. First, the same classification of drowsiness decided upon by the investigator(s) in recent EEG studies of each species in question was adopted for the present study. This step seemed justified because proposals for the classification of drowsiness tend to vary with the species, and when two or more investigators have studied the same species with the EEG, they have usually agreed on the classification of drowsiness. Second, because of the possibility that drowsiness has some equivalence to sleep, supplementary analyses were carried out in which 50% of the drowsiness in species in which it is prominent was treated as sleep. The details of these supplementary analyses are given below.

The review of the literature revealed some differences among investigators on procedures for scoring SWS time and PS time. In some species, sleep is highly fragmented, and there may be fairly rapid alternation of SWS, PS, and wakefulness. In scoring the EEG records of such species, investigators tend to differ on the length of the basic scoring interval. For example, some score by 20-sec epochs, others by 10-sec epochs. With long epochs, brief stage changes are overlooked. This difference in procedure may be a source of error in the data but was judged to be of minor importance. For some species it was possible to minimize such error by averaging the results obtained by different investigators. Investigators also differ when defining the length of the sleep cycle [62, 78, 138, 146]. In calculating cycle length, some include periods of arousal which are interspersed within extended periods of sleep, but others do not. The definition of cycle length adopted in the present study excludes arousal. Values including arousal were used only when a correction for arousal was not possible or when another report that excluded arousal was not available. Because it was not possible to correct for all the differences among investigators, the values for cycle length that appear in table I are not perfectly comparable.

In table I no genus is represented by more than one entry. In some instances, as previously mentioned, the results of two or more investigations of a single species were averaged. All of the data in table I are for sexually mature specimens except that some data for several primates, as indicated below, are for mixed groups of mature and somewhat immature specimens. Both sexes were represented in most studies, but the presence of both sexes was not required for the inclusion of findings in this study. Studies based on behavioral observations are identified as such in the list of sources below; otherwise, the use of EEG recordings can be assumed. In some EEG studies, electromyograms (EMGs) from the neck muscles and electrooculograms (EOGs) to detect eye movement were also recorded to aid in the identification of PS. The recordings or behavioral observations were continuous for 24-hour periods except where indicated otherwise. 24-hour recordings were not considered indispensable for species whose sleep is monophasic, i.e., concentrated during one portion of the day.

Sources for the Sleep Data²

Echidna (*Tachyglossus aculeatus*): five Ss, 2–5 days [8]. North American opossum (*Didelphis marsupialis*): for TST and PS, averages for five Ss, 1–3 days [140] and several Ss in an enclosure, 8 days by telemetric EEG [123]. For cycle length, average for five Ss [140] and for 11 or 12 Ss [120]. Water opossum (*Lutreolina crassicaudata*): 20 Ss, 5 days [4]. Phalanger (*Trichosurus vulpecula*): three Ss, several days [80]. Kangaroo (*Macropus rufus*): behavioral observations of two Ss in a zoo for 5.5 h during their principal sleep period on each of 4 days [35]. It appears that the kangaroo sleeps little, but no figure was adopted for TST because the observations were limited to a small portion of the day. Tenrec (*Tenrec ecaudatus*): several Ss in an enclosure, 8 days by telemetric EEG [123]. European hedgehog (*Erinaceus europaeus*): several Ss in an enclosure, 8 days by telemetric EEG [123]. Desert hedgehog (*Paraechinus hypomelas*): two Ss, 8–10 days [131]. Eastern American mole (*Scalopus aquaticus*): six Ss, 1–3 days [7]. Star-nosed mole (*Condylura cristata*): one S, 1 or 3 days [7]. Bats (*Myotis lucifugus* and *Eptesicus fuscus*): six Ss in each species, several days [28].

Tree shrew (*Tupaia glis*): six Ss, several days [18]. Slow Loris (*Nycticebus coucang*): six Ss, behavioral observations every 5 min for 3 days [133]. Galago (*Galago senegalensis*): 15 Ss, each with five EEG recording sessions of unspecified duration estimated at 11 h for the calculation of sleep quotas [19]. Owl monkey (*Aotus trivirgatus*): three Ss, 2 or more days [96]. Squirrel monkey (*Saimiri sciureus*): an average for three Ss from whom 5-min EEG recordings were obtained every 15 min during 12-hour sessions on 7 nights [1] and for an unspecified number of Ss studied for an unspecified number of days [96]. Results for PS time in these two studies differed so widely (27.8 and 7.8%) that it seemed inadvisable to include any figure. Vervet (*Cercopithecus aethiops sabaues*): four Ss, adults and sub-adults, for a total of eight recording sessions, 13.5 h each [22]. Patas monkey (*Erythrocebus patas*): four Ss, adults and subadults, for a total of 10 recording sessions, 13.5 h each [22]. Rhesus monkey (*Macaca mulatta*, *Macaca nemestrina*, and *Macaca radiata*): for TST and PS, averages based on six *nemestrina*, with two all-night recording sessions of unspecified duration for each animal [100], nine *radiata* with a total of 48 13-hour sessions [23], and 12 *mulatta*, some of them subadult, studied for at least 5 nights each, with recording sessions of 10.5 h [23, 24]. In these studies, the Ss either wore restraint collars or were confined to chairs. These studies were chosen in preference to others whose recording sessions were shorter and whose samples were less adult. For cycle length, an average for five Ss studied 6 h per night on 30 nights [147] and 10 Ss, studied for 7–9 h on a total of 70 nights [78], with some immature Ss in both studies. Baboon (*Papio papio*): for TST and PS, averages for seven Ss caged in their natural habitat, studied by telemetric EEG for several sessions of 11 h [94] and 10 Ss in a laboratory for a total of 13 telemetric recording sessions of unspecified duration estimated at 12 h [19]. Several studies based on wire recordings were disre-

² In the list of sources, the number of 'days' refers to the number of continuous 24-hour recording sessions per specimen. The term 'several' has been used to describe the number of specimens or the number of recording sessions when there was more than one but the precise number was not available. In a few instances published reports have been clarified by personal communications with investigators.

garded though their results were fairly consistent with the adopted data. For cycle length, seven Ss previously described, studied by telemetry [94]. Chimpanzee (*Pan troglodytes*): for TST and PS, a total of 7 days of telemetric EEG recordings for three Ss [21]. Cycle length was calculated from a representative diagram for one S in this study. Man: for TST, an average for eight or more overnight EEG recordings from 15 American Ss in a laboratory [62], questionnaire data on the 24-hour sleep patterns of 240 British Ss aged from 20 to the seventies [135], and questionnaire data for 257 Mexican Ss aged 20–80 [130] included to represent the polyphasic sleep patterns of some cultures. The PS% and cycle length are from HARTMANN [62]. PS time was calculated from the figures for TST.

Giant armadillo (*Priodontes giganteus*): three Ss, 3 days [4]. Nine-banded armadillo (*Dasypus novemcinctus*): five Ss, four for 1 day, one for 13 h [98]. The figures for PS are the highest estimates offered by the authors in the face of some uncertainties about scoring criteria for this species. Rabbit (*Oryctolagus cuniculus*): for TST and PS, averages of the data for nine intact Ss, total of 22 days [91], 38 ovariectomized Ss, up to 1 week each [73], and 12 ovariectomized Ss, 2 days [125]. The figure for cycle length was derived by averaging 39 min, as calculated from a representative diagram for one S [91] and 19 min (with wakefulness deducted) as calculated from data for an unspecified number of Ss [146].

Mountain beaver (*Aplodontia rufa*): several Ss in an enclosure, 8 days by telemetric EEG [123]. Yellow-bellied marmot (*Marmota flaviventris*): eight Ss, unspecified duration [124]. Ground squirrel (*Citellus tridecemlineatus*): six Ss, 2 days [138]. Arctic ground squirrel (*Citellus undulatus parryi*): nearly continuous behavioral observations at intervals of 15 min maximum on five Ss in an outdoor enclosure in continuous Arctic daylight for an average of 210 h/S [57]. Golden hamster (*Mesocricetus auratus*): for TST and PS, averages for six Ss, 2 days [138] and four Ss, 2 days [37]. Cycle length is as given by VAN TWYVER [138]. Mole rat (*Spalax leucodon*): five Ss, 3 days [72]. Rat (*Rattus norvegicus albinus*): for TST and PS, averages for six Ss, 2 days [138]; five Ss, each for several recording sessions of 22–23 h [60]; and for 12 Ss (aged 110, 114, and 413 days), 1 or 2 days each [151]. Cycle length is an average of the figure given by VAN TWYVER [1, 38] and the figure of 10 min as calculated (with wakefulness deducted) for an unspecified number of Ss studied by WEISS and ROLDAN [146]. Mouse (*Mus musculus*): for TST and PS, averages for six Ss, 2 days [138] and 37 Ss, 21 days each, representing two strains analyzed separately [137]. Cycle length is an average of the figure given by VAN TWYVER [138] and 7.0 min as calculated (with wakefulness deducted) for an unspecified number of Ss studied by WEISS and ROLDAN [146]. Guinea pig (*Cavia porcellus*): for TST, average for six Ss, unspecified number of days [95] and the midpoint of the range for two Ss described as well-habituated and studied up to 12 days [70]. For PS, averages of the data in the two aforementioned studies. For cycle length, average of 10 min (with wakefulness deducted) as given by PELLET and BERAUD [95] and 15.3 min for an unspecified number of Ss [11]. Chinchilla (*Chinchilla laniger*): six Ss, 2 days [138].

Gray wolf (*Canis lupus*): based on a representative 1-day record of behavioral observations and radio-transmitted heart rate for one of several Ss studied for several days in an outdoor enclosure in 24-hour arctic daylight [55]. Red fox (*Vulpes vulpes*): three Ss, 1 week [44]. Drowsiness in this species occupies 4.8 h daily in ad-

dition to SWS and PS. For supplementary calculations with TST adjusted to include 50% of drowsiness, the value for TST was 12.2 h and the value for the PS% was 19.7. Arctic fox (*Alopex lagopus*): based on a representative 1-day record of behavioral observations and radio-transmitted heart rate for one of several Ss studied for several days in 24-hour arctic daylight in an outdoor enclosure [55]. Raccoon (*Procyon lotor*): based on heart rates of one S in an outdoor enclosure sampled every 30 min for 2 weeks [56]. The use of heart rate data alone to judge sleep time in this instance seemed justified because concordance between heart rate and sleep behavior had been demonstrated in other species under similar conditions by the same investigators [55]. Cat (*Felis domestica*): averages for nine Ss, several days [46], eight Ss, 23 h each [127], and 12 Ss, 22 h each [136]. Quotas for 24 h were extrapolated from the data for shorter recording periods. Drowsiness in the cat occupies from 2 to 3 h daily in addition to SWS and PS [127] and may have been counted as sleep by DELORME *et al.* [46]. For supplementary calculations with TST adjusted to include 50% of drowsiness, a figure of 15.2 h for TST and 23.7 for the PS% was derived from the data reported by STERMAN *et al.* [127] and URSIN [136]. Jaguar (*Panthera onca*): two Ss, continuous behavioral observations for 2 days in a zoo [148].

Asian elephant (*Elephas maximus*): for TST, an average for five Ss observed in a stable on 9 nights by KURT [79] and data for 11 Ss observed in a stable 1 night by HEDIGER, as analyzed by KURT [79]. A figure of 2.25 h for TST given by BENEDICT [16] for a single S was disregarded. PS time is an average over 3 nights for one S observed in a zoo [63], with the occurrence of PS judged by eye movements and twitching. The PS% was derived by dividing the figure for PS time by TST. This method of arriving at the PS% may seem questionable because it combined data from different Ss, but in the absence of a definite figure for the adult elephant in any of the studies, the procedure seemed essential in order to take into account the great prominence of PS in this species, as noted by HARTMANN *et al.* [63]. For cycle length, one S observed for 3 nights in a zoo [63]. African elephant (*Loxodonta africana*): 13 Ss, observed for 1 night by HEDIGER as reported by KURT [79]. Horse (*Equus caballus*): for TST and PS, three Ss, several days [105]. Cycle length is from RUCKEBUSCH [104] and corresponds to a diagrammatic record for two Ss studied for 3 nights [107]. Drowsiness in the horse occupies 2 h/day according to RUCKEBUSCH [104] or perhaps 4 h, judging by an extensive behavioral study by STEINHART [126] based on 29 Ss for several days each. Both estimates of drowsiness were taken into account in supplementary calculations with TST quotas adjusted to include 50% of drowsiness. The adjusted figure for TST was 4.3 h and the PS% was 20.4. Donkey (*Equus asinus*): three Ss, several days [102]. The figure for TST appears to exclude drowsiness, for which no estimate was available. Brazilian tapir (*Tapirus terrestris*): Continuous behavioral observations of two Ss in a zoo, 1 day, with PS judged by twitching [148].

Roe deer (*Capreolus capreolus*): continuous behavioral observations of two Ss in an enclosure with the aid of infrared equipment. TST was calculated from data for 20–22 days, omitting days when sleep was disturbed [32]. Giraffe (*Giraffa camelopardalis*): behavioral observations of three Ss, 14 nights each [69]. Head resting on the ground with neck bent was assumed to be a sign of PS. Okapi (*Okapi johnstoni*): one S, 6 nights. Neck bent, with head resting between hind quarter and thigh,

was assumed to represent PS [69]. Goat (*Capra hircus*): five Ss, several days to 2 months [102]. The goat was reported to sleep 8 h, including drowsiness. In the light of more recent reports on other ruminants, the ratio of SWS and drowsiness was assumed to be the same as in the sheep, and TST was calculated on this basis. In supplementary calculations with TST adjusted to include 50% of drowsiness, the figure for TST was 6.3 h and the PS% was 7.9. All figures for PS were calculated from data in the report. Sheep (*Ovis aries*): three Ss, several days [105]. According to the same study, drowsiness in the sheep occupies about 4 h/day. In supplementary calculations with TST adjusted to include 50% of drowsiness, the figure for TST was 5.9 h and the PS% was 10.2%. Cow (*Bos taurus*): for TST and PS, three Ss, several days [105]. According to the same study, drowsiness in the cow occupies about 7 h/day. In supplementary calculations, with TST adjusted to include 50% of drowsiness, the figure for TST was 7.5 h and the PS% was 9.3. A frequently quoted report by BALCH [14] that the cow sleeps about 36 min/day was disregarded because BALCH appears unwittingly to have measured only PS time. The figure for cycle length is based on three Ss [108].

Some information which was available on the sleep of several species was not judged suitable for inclusion as data in the present study. Based on recordings from one immature S, SHURLEY *et al.* [119] have reported 5.3 h of sleep per day in the pilot whale (*Globicephalus scammoni*), including 0.1 h of PS. Based on recordings from three immature Ss, RUCKEBUSCH [105] has reported that the pig (*Sus scrofa*) obtains 7.8 h of sleep per day, including 1.7 h of PS but not counting 5.1 h of drowsiness. Because of the immaturity of the Ss, the foregoing findings were not included as data. However, on the basis of the ontogenetic patterns in all other mammalian species, it can be assumed that TST and PS time would be somewhat less in adult whales and pigs.

VAN TWYVER and ALLISON [139] have reported that convincing EEG signs of sleep are absent in the short-tailed shrew (*Blarina brevicauda*), raising the possibility that this species does not sleep. On the other hand, ROOD [101] has described sleeping postures in this species, and CROWCROFT [43] has noted the occurrence of sleep in other members of the same family. It therefore appears that shrews sleep, but how much remains to be determined. SCHALLER's [113, 114] naturalistic observations of the gorilla (*Gorilla gorilla beringei*) have suggested to some writers that this species may sleep 17 h/day [76, 121], but this estimate assumes that the gorilla sleeps continuously except during daylight. In the absence of any nighttime observations, such estimates are questionable, and for this reason, the gorilla was not included here. BEEBE [15] observed one three-toed sloth (*Bradypus cuculliger cuculliger*) continuously by day and intermittently at night for 1 week in its natural habitat. He estimated that the sloth sleeps 18.5 h/day. However, a radiotelemetry study of activity patterns in 15 three-toed sloths (*Bradypus infuscatus*) [128] indicates that BEEBE's estimate is exaggerated. Therefore no data for the sloth was included.³

³ The review of the literature on sleep quotas was completed in August 1974. Reports that came to the attention of the authors after this cut-off point could not be included in the data analysis. Some earlier studies may have escaped the attention of the authors.

The data on life spans are mainly from compilations by COMFORT [39], CRANDALL [42], and SACHER [111]. The longest life span accepted by any one of these writers was the one adopted. Primary reliance on these writers served to screen out unreliable reports of longevity. Supplementary sources were: WALKER *et al.* [142] for the kangaroo, phalanger, marmot, red fox, roe deer, and sheep; GODFREY and CROWCROFT [59], whose estimate for *Talpa europea* was adopted for the moles in this study; HERREID [66] for the bats; and COMFORT [38] for the cow. The value given by SACHER [111] for *Tupaia tana* was adopted for the tree shrew. The figure for the chimpanzee is from unpublished data [53]. Although longer life spans have been recorded for humans, 100 years was adopted as an estimate of what the maximum might be if environmental conditions for humans were the same as those of captive or domesticated animals.

Virtually all of the data on brain weight are from compilations by SACHER [111], QUIRING [99], COUNT [41], and VON BONIN [141]. These sources also provided the corresponding data on body weight. The figures for the rat are from DONALDSON [48]. In some instances, the figures for two or more specimens were averaged, but whenever table II contains figures both for brain weight and body weight, they are for the same specimens. All specimens were described as adult, but some do not appear to have been fully grown. As a result, because brain weight approaches its maximum earlier than body weight, the ratio of brain weight to body weight probably is slightly exaggerated. In the absence of brain weights for some species, substitute values were adopted as follows: *Eptesicus serotinus* for *Eptesicus fuscus* (big brown bat); *Tupaia javanica* for *Tupaia glis* (tree shrew); *Cricetus cricetus* for *Mesocricetus auratus* (golden hamster); *Spalax hungaricus* for *Spalax leucodon* (mole rat). The values for the rhesus monkey are for *nemestrina*. For some species, no figures on brain weight were available. In these cases, only figures for body weight appear in table II. These are for average-sized specimens and were drawn from various compilations.

Oxygen consumption rates were drawn from a number of compilations and reports. Most figures represent basal rates, i.e., rates measured postabsorptively at metabolically indifferent temperatures in animals at rest or minimally active. However, some rates can more properly be described as resting rates because not all of the measurement criteria were met. For some species, considerable variation was found in the reports of different investigators, but as a rule, no attempt was made to reconcile or to 'average out' the differences. In adopting rates, preference was given on a methodological basis to those presented by KLEIBER [74]. Methodological criteria were also employed in some additional instances. Some departures from the expected relationship between oxygen consumption rates and body weights can be recognized in table II. Sources follow: Echidna: SCHMIDT-NIELSEN *et al.* [117]; North American opossum, nine-banded armadillo, and mole rat: McNAB [83]; Eastern American mole: PEARSON [93]; European hedgehog: MORRISON [87]; little brown bat, estimated from HOCK's data [68]; owl monkey and Arctic fox: SCHOLANDER *et al.* [118]; squirrel monkey and red fox: ALTMAN and DITTMER [10]; ground squirrel: FOLK, jr. [54]; Arctic ground squirrel: SCHOLANDER *et al.* [118]; hamster: ADOLPH and LAWROW [3]; elephant: BRODY [31]; horse and goat; ; BENEDICT [17]. The figure for the raccoon is for *Procyon cancrivorus* [118], and the figure for the wolf is

based on a large dog [74]. For the remaining species the data are from KLEIBER [74]. A caloric equivalent of 4.8 kilocalories/liter oxygen was assumed in converting the caloric values given in some reports to rates of oxygen consumption.

The data on gestation period are from compilations by WALKER [142], ALTMAN and DITTMER [9], BURTON [33], and COCKRUM [36]. In the nine-banded armadillo and in the roe deer there are delays of implantation which were not included in the figures for these species.

Statistical Analyses

The principal correlational analyses were carried out on the combined data for 53 species. Statistical tests on the data in tables I and II revealed that the values of all variables except TST and SWS time were skewed at a statistically significant level ($p < 0.05$). To avoid the effects of skewness on the magnitude of correlation coefficients, the common logarithms of the values in tables I and II were used for all variables except TST and SWS time. Details of the rationale for these and other statistical procedures are in McNEMAR [85]. All statistical tests were two-tailed. As can be seen in tables I and II, the number of species for which there was data was not the same for all analyses. When not given in the report of results, the *N*s for various calculations can be determined by reference to the tables.

Pearson product moment correlation coefficients were calculated for all pairs of variables shown in tables I and II, including SWS time. The relative strengths of the correlations between the various sleep parameters and the other constitutional variables were assessed by means of *t* tests. Relationships among sleep parameters which assumed importance were similarly tested. Partial correlation coefficients were calculated to test for the strength of relationships between pairs of variables while holding constant the contributions to such relationships by other variables. In this procedure, the variable held constant had to be theoretically capable of exerting a causal influence upon both of the other variables in the comparison. In other words, it was possible to calculate the partial correlation of Variable A and B with Variable C held constant only when Variable C stood in a causal relationship with respect to both Variables A and B. In selected instances, when Variable C stood in a causal relationship with respect to only one member of a pair of variables, *part* correlation coefficients were calculated. Least-squares regression equations were calculated to describe further the relationships between sleep parameters that assumed major importance and the principal constitutional variables, and multiple regression analysis was employed to assess the independent contributions of these constitutional variables.

Multivariate analyses that dealt with both metabolic rate and brain weight were carried out only with the estimates of metabolic rate based on body weight. In these analyses it was necessary to use data on metabolic rate and brain weight based on the same specimens. No information on brain weight was available for the specimens used in calorimetric determinations of oxygen consumption rates. Because of controversy regarding the significance of drowsiness, the foregoing calculations were repeated with modified values for TST, SWS time and PS% as described above.

Because there is evidence suggesting that hibernation promotes longevity [25], correlations between sleep parameters and life spans were also calculated with data

omitted for species that hibernate for significant periods (echidna, tenrec, hedgehogs, squirrels, marmot, and hamster).

Because some orders (e.g. rodents) are relatively easy to study, they were disproportionately represented among the 53 species. As a check on the possible effect of this sampling bias, supplementary analyses were carried out with the family rather than individual species as the unit of study. This procedure equalized somewhat the representation of different orders. The validity of this procedure was suggested by inspection of the data, which indicated that members of a family tend to have similar sleep characteristics, often in spite of large differences in constitutional variables (note for example, the opossums, bats, armadillos, and artiodactyls). For these analyses, mean values of the sleep parameters were calculated for families represented by more than one species. Families represented by a single species were simply represented by the data for that species. If there was no data for one of several species in a family, the data for the remaining species were used or averaged. With respect to the constitutional variables, the same procedures seemed appropriate only with respect to brain weight and metabolic rate as estimated from body weight, for which the data were ample. Correlations of the sleep parameters with brain weight and metabolic rate were calculated for comparison with the correlations found in the data for the 53 species treated individually.

Although the data for individual orders were not extensive, analyses of within-order relationship between selected variables and of between-order differences on sleep parameters were carried out to obtain a tentative picture of the role of individual orders. Within-order relationships were assessed by means of correlation coefficients. For these analyses, logarithmic values were used only for brain weight and body weight since the values of sleep parameters within orders were not markedly skewed. Between-order differences were assessed by one-way analyses of variance followed by the Scheffé method of comparing group means when a significant difference among orders was found. Because the analysis of variance is robust with respect to minor departures from the assumptions of normality and homogeneity of variance, the original values of the sleep parameters were used in these analyses. Analyses of covariance were desirable to test for differences between orders adjusted for effects by the correlations which were found between most of the sleep parameters and brain weight and body weight. However, the data did not fulfill the requirements for such analyses because of the marked between-order differences on brain weight and body weight and because of inconsistent relationships which were found within orders between these variables and the sleep parameters.

Results

Table III presents the correlation coefficients based on the data for all 53 species and for all variables listed in tables I and II with the exception of oxygen consumption rate. In the 29 species for whom the necessary data were available, oxygen consumption rate correlated 0.95 with metabolic rate as estimated from body weight. When calculated for the same

Table III. Correlation coefficients among sleep parameters and other constitutional variables

	SWS time	PS time	PS %	Cycle length	Life span	Meta- bolic rate	Brain weight	Ges- tation period
TST	0.96** (39)	0.76** (38)	0.06 (38)	-0.66** (23)	-0.52** (43)	0.64** (49)	-0.71** (38)	-0.69** (41)
SWS time		0.58** (38)	-0.17 (38)	-68.0** (23)	-0.45* (34)	0.67** (39)	-0.70** (30)	-0.58** (33)
PS time			0.67** (38)	-0.39 (23)	-0.45* (35)	0.48* (40)	-0.54* (31)	-0.64** (35)
PS %				0.27 (24)	-0.05 (35)	-0.12 (40)	0.10 (31)	-0.09 (35)
Cycle length					0.81** (24)	-0.83** (24)	0.92** (22)	0.79** (24)
Life span						-0.68** (46)	0.85** (37)	0.73** (41)
Metabolic rate							-0.96** (40)	-0.77** (45)
Brain weight								0.85** (38)

The number of cases for each coefficient is in parentheses. Logarithmic transformations were used for all variables except TST and SWS time. Metabolic rate was derived from body weight.

* $p < 0.01$; ** $p < 0.001$.

29 species, the correlation between TST and oxygen consumption rate was 0.58 ($p < 0.001$) and the correlation between TST and metabolic rate as estimated from body weight was 0.65 ($p < 0.001$). Similar comparisons were carried out for the other sleep parameters. In the identical set of species ($n = 24$), SWS time correlated 0.63 ($p < 0.001$) with oxygen consumption rate and 0.73 ($p < 0.001$) with metabolic rate estimated from body weight. The corresponding correlations for PS time based on 23 species were 0.38 (NS) and 0.44 ($p < 0.05$). For PS%, based on 23 species, they were -0.34 and -0.35 (NS). For cycle length, based on 17 species, they were 0.90 ($p < 0.001$) and 0.90 ($p < 0.001$).

As table III shows, all sleep parameters except PS% were significantly correlated with all the other constitutional variables, but cycle length cor-

related with these variables in a manner opposite to that of the other sleep parameters. PS% was significantly correlated only with PS time. Table III gives preliminary indications that a substantial amount of the variance in most of the sleep parameters may be predicted by the constitutional variables. The square of the correlation coefficient (the coefficient of determination) gives the amount of variance that can be accounted for by a correlation. Thus metabolic rate as estimated from body weight may account for 40% of the variance in TST and 45% of the variance in SWS time. Brain weight may account for 49% of the variance in these sleep parameters. Metabolic rate and brain weight, respectively, can account for 69 and 85% of the variance in cycle length. However, these results must be interpreted in conjunction with the results of additional analyses, described below, which take into account the effects of intercorrelations among the sleep parameters and among the other constitutional variables.

With the exclusion of data for species that hibernate, the correlation of TST and life span was -0.59 ($p < 0.001$). Other correlations with life span were -0.59 ($p < 0.001$) for SWS time, -0.43 ($p < 0.01$) for PS time, and 0.03 (NS) for PS%. Thus the relationships between life span and measures of sleep time were essentially unaltered when the effect of hibernation on life span was controlled.

When based on all of the available data, as shown in table III, the statistically significant correlations between cycle length and the constitutional variables, in absolute terms, were considerably greater than the corresponding correlations between the constitutional variables and the other sleep parameters. However, when each of the comparisons between correlation coefficients was based on the same set of cases in order to control for a possible effect by the number of species with available data, *t* tests revealed that the coefficients for cycle length were significantly greater only in some instances. The correlation between cycle length and life span (0.82) was significantly greater than the correlation of life span with TST (-0.49), SWS time (-0.48), or PS time (-0.35) ($t = 3.17, 3.38$, and 4.27 , respectively; in the first two comparisons, $p < 0.01$; in the last, $p < 0.001$; $n = 23$). The correlation between cycle length and brain weight (0.92) was significantly greater than the correlation of brain weight with TST (-0.74), SWS time (-0.77), or PS time (-0.44) ($t = 2.73, 2.35$, and 4.02 , respectively; in the first two comparisons, $p < 0.05$; in the last, $p < 0.001$; $n = 22$). However, the correlation between cycle length and metabolic rate estimated from body weight (-0.87), though significantly greater than the correlation between PS time and metabolic

rate (0.46) ($t = 3.94$; $p < 0.001$), was not significantly greater than the correlations of metabolic rate with TST (0.79) and SWS time (0.82) ($t = 1.14$ and 0.74 , respectively; $n = 23$ in all comparisons). These results were essentially the same when the analyses were based on oxygen consumption rates in 17 species. The correlation between cycle length and gestation period (0.78) proved not to be significantly greater than the correlation of gestation period with TST (-0.73), SWS time (-0.69), or PS time (-0.59) ($t = 0.96$, 1.10 , and 1.52 , respectively; $n = 23$ in all comparisons). In summary, therefore, cycle length was more strongly related to life span and brain weight than any of the other sleep parameters, but was not more strongly related to metabolic rate or gestation period.

Other comparisons which controlled for sample composition revealed the following: the correlation of SWS time and metabolic rate estimated from body weight (0.67) was significantly greater than the correlation of PS time (0.40) ($t = 2.35$; $p < 0.05$, $n = 38$), but the correlation of SWS time with oxygen consumption rates (0.64) did not significantly exceed the correlation of PS time with oxygen consumption (0.38) ($t = 1.76$, $n = 23$). This difference apparently stemmed from the difference in size and composition of the subsamples. There was no significant difference between the correlations of SWS time and PS time with brain weight ($r = -0.70$ and -0.49 , respectively; $t = 1.78$; $n = 30$), and when compared on the basis of the same number of cases, these two variables correlated at almost identical levels with life span and gestation period (with life span, $r = -0.40$ and -0.43 , respectively, and with gestation period, $r = -0.58$ and -0.60 , respectively, $n = 33$ in both comparisons). Although SWS time correlated more strongly than PS time with cycle length in the same set of cases ($r = -0.68$ and -0.39 , respectively), the difference between them was not significant ($t = 1.93$; $n = 23$).

Table IV presents partial correlation coefficients which were calculated to control for the effects of intercorrelations among the principal variables. The correlations of life span with TST, SWS time, and PS time were not significant when metabolic rate or brain weight was held constant, making it necessary to conclude that there is no relationship between these sleep parameters and life span that is independent of metabolic rate or brain weight. Cycle length, however, remained significantly correlated with life span when metabolic rate was held constant but not when brain weight was held constant, indicating that the relationship between cycle length and life span is independent of metabolic rate but not of brain weight. Essentially the same results were obtained when oxygen

Table IV. Partial correlation coefficients based on sleep parameters and other constitutional variables

Variable A	Variable B	Variable C	A ^r , B	A ^r , C	B ^r , C	AB ^r , C	n	p
TST	life span	metabolic rate	-0.52	0.65	-0.69	-0.13	42	0.41
SWS time	life span	metabolic rate	-0.45	0.71	-0.69	0.07	34	0.69
PS time	life span	metabolic rate	-0.45	0.46	-0.69	-0.20	35	0.25
Cycle length	life span	metabolic rate	0.81	-0.83	-0.74	0.52	24	0.01
TST	life span	brain weight	-0.58	-0.71	0.85	0.05	36	0.76
SWS time	life span	brain weight	-0.56	-0.71	0.85	0.14	29	0.46
PS time	life span	brain weight	-0.43	-0.53	0.85	0.05	30	0.80
Cycle length	life span	brain weight	0.85	0.92	0.85	0.29	22	0.20
TST	brain weight	metabolic rate	-0.71	0.70	-0.96	-0.16	38	0.33
SWS time	brain weight	metabolic rate	-0.70	0.73	-0.95	-0.02	30	0.89
PS time	brain weight	metabolic rate	-0.54	0.54	-0.96	-0.09	31	0.65
Cycle length	brain weight	metabolic rate	0.92	-0.87	-0.96	0.60	22	0.004
TST	cycle length	metabolic rate	-0.66	0.79	-0.87	0.09	23	0.70
TST	cycle length	brain weight	-0.66	0.74	0.92	0.09	22	0.68
SWS time	PS time	metabolic rate	0.58	0.67	0.40	0.46	38	0.004
SWS time	PS time	brain weight	0.63	-0.70	-0.49	0.46	30	0.013
TST	gestation pd	metabolic rate	-0.70	0.73	-0.78	-0.30	41	0.06
SWS time	gestation pd	metabolic rate	-0.58	0.76	-0.76	-0.01	33	0.95
PS time	gestation pd	metabolic rate	-0.64	0.54	-0.79	-0.41	35	0.015
Cycle length	gestation pd	metabolic rate	0.79	-0.83	-0.76	0.44	24	0.037
TST	gestation pd	brain weight	-0.68	-0.71	0.85	-0.21	36	0.23
SWS time	gestation pd	brain weight	-0.58	-0.70	0.84	0.00	30	0.98
PS time	gestation pd	brain weight	-0.60	-0.54	0.85	-0.32	31	0.09
Cycle length	gestation pd	brain weight	0.79	0.92	0.86	-0.04	22	0.86

Logarithmic transformations were used for all variables except TST and SWS time. Metabolic rate was derived from body weight. The partialing out of metabolic rate in the calculation of partial correlations between brain weight and other variables was justified by the dependence of brain weight on body weight.

consumption rates were used for metabolic rate instead of estimates based on body weight. The results were also essentially the same when the foregoing analyses were limited to the identical set of cases ($n = 22$), demonstrating that the difference between the results for cycle length and for the other sleep parameters was not based on any difference in the composition of the samples on which the analyses were based.