Sleep in Mammals – Ecological and Constitutional Correlates

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as those of clone C. The effectiveness of the clone B type of mechanism for protecting males against cannibalism, therefore, probably depends both on the frequency of encounters with cannibals which do attack them and on the voracity of such cannibals.

Males of clone C are readily attacked by cannibalistic female, especially campanulate, clonemates but have structural adaptations which protect them from being captured. A mechanism by which campanulates avoid attacking male clonemates may not have developed in clone C for several reasons. First, campanulates seem to be rare in this clone (3) and so may co-occur with male clonemates infrequently. Second, the great voracity of clone C campanulates might not be compatible with subtle feeding preferences.

It must be emphasized that male anticannibalism devices have been investigated only in these two quite distinct clones. The extent to which the development of the different protective mechanisms may be typical of, and effective within, the respective taxa—probably races or possibly closely related species (7)—is not known.

The failure of clone B males to trigger tactile feeding responses in cannibalistic female clonemates appears to be a type of defense against cannibalism not yet reported in other predatory aquatic organisms. It is probably an efficient adaptation because it operates very quickly without involving handling, and possibly damage, of the male by the female. In *Asplanchna*, it may also permit further reduction in male size and structural complexity.

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7. Clones B and C, respectively, were designated as clones 12C1 and 10C6 of *A. sieboldi* by C. W. Birky, Jr., who collected them from a sewage disposal plant in Davis, Calif., in the summer of 1967. However, the females of clone 12C1 resemble those of the questionable species *A. intermedia* in jaw structure [J. J. Gilbert, *Physiol. Zool.* **41**, 14 (1968)]; clone 10C6 is clearly *A. sieboldi* in all respects. Reciprocal matings and cross-fertilizations occur, but the viability of the resting eggs so produced is not known (C. W. Birky, Jr., unpublished results). The clones certainly belong to separate races and perhaps even species.
8. Diets consisted of the ciliate *Paramecium aurelia* with $10^{-7}M$ *d*-α-tocopherol or the rotifer *Brachionus calyciflorus* together with its food organism, *Euglena gracilis*, strain Z.
9. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969).
10. *HP-65 Stat Pac 1* (Hewlett-Packard, Cupertino, Calif., 1974).
11. The cruciform morphotype of clone B is unstable, rapidly transforming to the campanulate morphotype or to cruciform-campanulate intermediates (3), and was not studied.
12. Supported by NSF grant GB-31282, PHS grant 1 R01 HD 08210, and PHS research career development award K04-GM-70557. I thank M. Bean for expert technical assistance and T. M. Frost, J. R. Litton, Jr., P. L. Starkweather, and W. C. Kerfoot for improving the manuscript.

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Abstract. *The interrelationships between sleep, ecological, and constitutional variables were assessed statistically for 39 mammalian species. Slow-wave sleep is negatively associated with a factor related to body size, which suggests that large amounts of this sleep phase are disadvantageous in large species. Paradoxical sleep is associated with a factor related to predatory danger, which suggests that large amounts of this sleep phase are disadvantageous in prey species.*

Every mammalian species studied in the laboratory spends at least some time asleep, and some species spend a major portion of their lives in this state (1). We may assume that sleep serves some (as yet unknown) biological function, but, if so, why do sleep requirements vary so much from species to species? By correlating sleep habits and other characteristics of species adapted to a wide variety of ecological niches it may be possible to clarify the significance of sleep in the life of mammals.

Comparative sleep data are currently available for fewer than 1 percent of the total species of mammals. However, Zepelin and Rechtschaffen (2) computed correlations between some sleep characteristics (such as total sleep time per day) and constitutional variables (such as lifespan) and found them to be robust, which suggests that the available data are sufficient to allow at least a preliminary analysis of the biological forces that shape, and are shaped by, sleep.

However, the Zepelin-Rechtschaffen analysis did not include environmental or ecological influences, which may affect sleep (1, 3, 4). In one analysis (4) species were divided roughly into "good" and "poor" sleepers. Good sleepers sleep at least 8 hours per day, sleep read-

ily in the laboratory, and seem to need a great deal of sleep. Conversely, poor sleepers tend to sleep less and require long periods of adaptation to the laboratory before stable sleep habits are observed. These groups seem ecologically different in two ways. Predators (such as cats) are good sleepers, whereas species subject to heavy predation (such as rabbits) are poor sleepers. Second, species that sleep in reasonably secure places (such as bats) tend to sleep more than species that sleep in the open (such as sheep). We therefore analyzed the interrelationships between sleep, constitutional characteristics, and ecological influences and found that both constitutional and ecological influences are important predictors of the amount and type of sleep obtained by mammals.

This analysis was based on data for 39 species distributed over 13 orders. Incomplete data for 21 additional species were not suitable for the multivariate analyses reported here. The sleep variables we evaluated are the amounts per day of the two qualitatively different stages (5): slow-wave sleep (SWS) is characterized by high-amplitude slow waves in the electroencephalogram and by behavioral and autonomic nervous system quiescence; paradoxical sleep

Table 1. Correlation coefficients for sleep, ecological, and constitutional variables (16). For all $R > .51$, $P < .001$. Abbreviations: SWS, slow wave sleep; PS, paradoxical sleep; L, life-span; w_b, body weight; w_{br}, brain weight; t_g, gestation time; P, predation index; S, sleep exposure; D, overall danger.

Vari-ables	Correlation coefficients								
	SWS	PS	L	w_b	w_{br}	t_g	P	S	D
SWS	1.000	.582	−.377	−.712	−.679	−.589	−.369	−.580	−.542
PS		1.000	−.342	−.370	−.435	−.651	−.536	−.591	−.686
L			1.000	.685	.777	.682	.018	.518	.226
w_b				1.000	.945	.692	.253	.662	.432
w_{br}					1.000	.781	.192	.624	.377
t_g						1.000	.158	.588	.363
P							1.000	.680	.930
S								1.000	.819
D									1.000

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(PS) is characterized by a low-voltage electroencephalogram, brief movements of the extremities and facial muscles, autonomic irregularity, and, in man, dreaming (6). Four constitutional variables were evaluated: life-span in years, body weight in kilograms, brain weight in grams, and gestation time in days (7).

The severity of predation and safety of sleeping place were inferred from field observations in the literature (8). Species were rated according to a five-point scale on the extent to which they are preyed upon; a score of 1 indicated minimum predation. On a sleep exposure scale, species that usually sleep in a burrow, den, or other well-protected place were assigned a value of 1, and species that sleep in maximally exposed places were assigned a value of 5. A third five-point scale, called overall danger, provided a general estimate of predatory danger. This scale took into account the other two ecological estimates but was not simply a linear combination of them. For example, species which sleep in maximally exposed places (and hence were assigned a score of 5 on the sleep exposure scale) were nevertheless assigned a score of 1 on the overall danger scale if field observations indicated that they were rarely preyed upon (and hence were assigned a score of 1 on the predation index).

There are negative correlations between SWS and PS and all the constitutional and ecological variables, and all the constitutional variables are positively correlated with one another (Table 1). The correlations by themselves, however, do not reveal the pattern of relationships between variables, nor do they indicate those variables that may be important in accounting for sleep variability.

Factor analysis by principal components was used to explore the pattern of relationships between variables (9, 10). Two significant factors (eigenvalues greater than one) emerged. Varimax rotation (11, 12) yielded the factor pattern shown in Table 2. The first factor has strong loadings from the constitutional variables related to body size, and hence might be called a "size" factor. There is a moderate negative loading from SWS since larger species spend less time in SWS (Table 1). There is also a modest loading from sleep exposure, reflecting the fact that it is more difficult for larger species to use safe refuges such as trees or holes. The second factor, which might be called a "danger" factor, has strong positive loadings from the ecological variables and a negative loading from PS; that is, greater predatory danger is

Table 2. Factor analysis of sleep, ecological, and constitutional variables. Sorted, rotated factor loadings are shown; high loadings on each factor are in boldface type. The size factor accounts for 44.2 percent of the total variance, and the danger factor accounts for 36.2 percent.

Variables	Factors	
	Size	Danger
Brain weight	**.942**	.198
Body weight	**.882**	.258
Life-span	**.862**	.016
Gestation time	**.841**	.244
SWS	**−.630**	−.478
Sleep exposure	.523	**.738**
Overall danger	.190	**.964**
Predation index	−.044	**.957**
PS	−.393	**−.689**

associated with less PS. These two factors account for over 80 percent of the total variance and thus provide an efficient summary of the relationships between variables (Table 2). "Danger" is independent of "size" since the varimax method of rotation yields factors that are necessarily uncorrelated. Figure 1 summarizes the similarities and differences between species with respect to these factors.

To determine the variables that predict sleep variability, we carried out stepwise multiple regression analysis, in which SWS or PS were predicted (dependent) variables and the constitutional and ecological measures were predictor (independent) variables (9, 13). For SWS, the multiple regression equation is

$$SWS = 11.7 - (1.82 \pm 0.37) \log w_b - (0.799 \pm 0.33) D \qquad (1)$$

where w_b is body weight and D is overall danger. As $R = .76$, body weight and overall danger in combination account for 58 percent of the variability in SWS (that is, $R^2 = .58$). Addition of other variables to the regression equation did not significantly improve prediction of SWS. The best predictor of SWS is body weight; the negative correlation between these variables suggests that large amounts of SWS are adaptive in small species. However, brain weight is an equally good predictor when inserted into Eq. 1 in place of body weight ($R = .75$). Indeed, any biological parameter that is highly correlated with body weight might be a good predictor of SWS. Basal metabolic rate is another im-
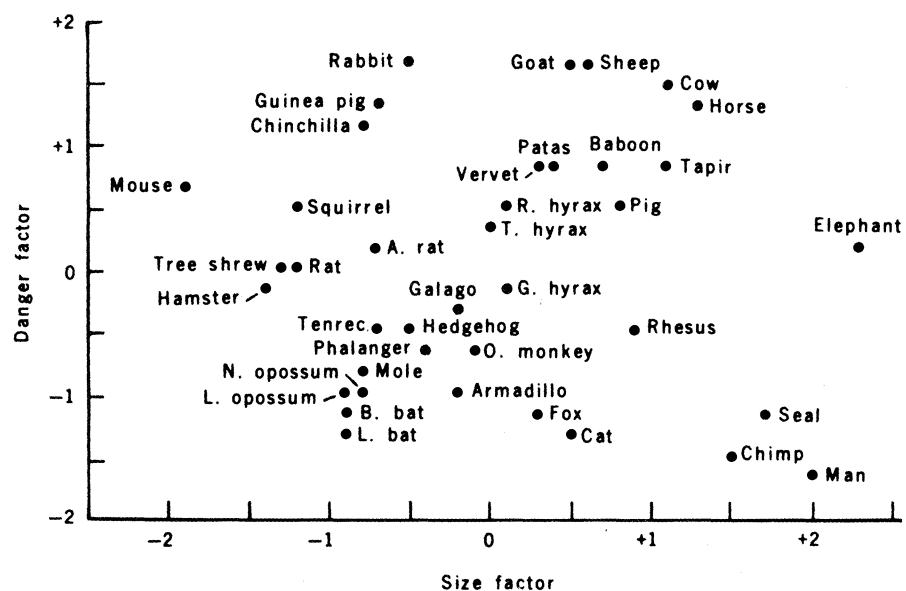

Fig. 1. Factor scores ($\overline{X} = 0$, S.D. = 1) for 39 species used in the factor analysis of Table 2. Smaller species appear to the left, larger species to the right. Species heavily preyed upon appear at the top, those less subject to predation at the bottom. Some clusters are perceptible, for example domesticated farm animals (goat, sheep, cow, horse), small surface-dwelling herbivores (rabbit, guinea pig, chinchilla), and African savanna primates (vervet, patas, baboon). The species are: African giant pouched rat, *Cricetomys gambianus*; armadillo, *Dasypus novemcinctus*; baboon, *Papio papio*; big brown bat, *Eptesicus fuscus*; cat, *Felis domestica*; chimpanzee, *Pan troglodytes*; chinchilla, *Chinchilla laniger*; cow, *Bos taurus*; elephant, *Elephus maximus*; fox, *Vulpes vulpes*; galago, *Galago senegalensis*; goat, *Capra hircus*; gray hyrax, *Heterohyrax brucei*; guinea pig, *Cavia porcellus*; hamster, *Mesocricetus auratus*; hedgehog, *Erinaceus europaeus*; horse, *Equus caballus*; little brown bat, *Myotis lucifugus*; little water opossum, *Lutreolina crassicaudata*; man, *Homo sapiens*; mole, *Scalopus aquaticus*; mouse, *Mus musculus*; North American opossum, *Didelphis marsupialis*; owl monkey, *Aotus trivergatus*; patas, *Erythrocebus patas*; phalanger, *Trichosurus vulpecula*; pig, *Sus scrofa*; rabbit, *Oryctolagus cuniculus*; rat, *Rattus norvegicus*; rhesus, *Macaca mulatta*; rock hyrax, *Procavia habessinica*; seal, *Halichoerus grypus*; sheep, *Ovis aries*; squirrel, *Citellus tridecemlineatus*; tapir, *Tapirus terrestris*; tenrec, *Tenrec ecaudatus*; tree hyrax, *Dendrohyrax validus*; tree shrew, *Tupaia glis*; vervet, *Cercopithecus atheops*.

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portant parameter that is highly correlated with body weight. Measurements of basal metabolic rate were not available for enough species ($N = 25$) to warrant inclusion in the multivariate analyses. However, for these species the correlations of metabolic rate with body weight and with SWS were $-.95$ and $.63$ respectively, which suggests that metabolic rate is as good a predictor of SWS as body weight. Zepelin and Rechtschaffen (2) proposed an association between SWS and metabolic rate whereby SWS provides a mechanism for enforcing rest and hence conserving energy. Such a mechanism was assumed to be especially important for small species because of their high metabolic rates. Although this interpretation provides a parsimonious explanation for the relationship between body weight and SWS, the converse interpretation should also be considered, namely that large amounts of SWS would be disadvantageous for large species for two reasons. (i) The largest species in this sample of mammals are herbivores, which presumably must spend large amounts of time foraging for food. (ii) Overall danger is the other predictor of SWS in the regression equation, and large herbivores are generally subject to heavy predation. Thus these two influences may oblige large herbivores to spend minimal time in SWS.

A different pattern of predictor variables emerged for PS. The multiple regression equation is

$$\text{Log PS} = 1.07 - (0.109 \pm 0.022)\,D$$
$$- (0.300 \pm 0.068)\log t_g \quad (2)$$

where D is overall danger and t_g is gestation time. Overall danger and gestation time in combination account for 66 percent of the variability in PS ($R = .81$). The best predictor of PS is overall danger. The negative correlation between these variables suggests that large amounts of PS are disadvantageous in species subject to heavy predation. During PS, animals are minimally responsive to external stimuli (14) and, hence, might be more vulnerable to predation. The inclusion of gestation time in the multiple regression equation is surprising. Partial correlation analysis shows that the negative correlation between PS and gestation time is independent of the influence of other variables. Since some prey species (such as guinea pigs), have longer gestation times than would be predicted from their body weights, the strong relationship between PS and gestation time may reflect another aspect of the sensitivity of PS to predatory danger (15). Adding other variables to Eq. 2 did not significantly improve prediction of PS.

Thus, two factors account for much of the interspecies variability of sleep in mammals; one is related to body size and the other reflects the degree to which species must cope with predatory danger. The first factor is associated with SWS, whereas the second is associated with PS. To oversimplify somewhat, one might regard SWS as being associated with constitutional or endogenous influences, whereas PS is associated with ecological or exogenous influences.

These conclusions are subject to three qualifications. (i) They apply only to interspecific comparisons; whether the same relationships hold between individuals of a species is unknown. (ii) Sleep is an integral part of the adaptation of a species to differing habitats and ways of life. The causal relationships between sleep and other variables are difficult to determine from this correlational analysis, which merely identifies some of the biological influences or processes with which sleep may interact. (iii) Only about 60 percent of the variance in SWS and PS can be accounted for by the variables considered here. Discovery of additional relevant variables and study of additional species will be required for a comprehensive picture of the natural history of sleep.

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6. Other common measures of sleep include total sleep time (TST), PS percent (PS/TST × 100), and sleep cycle time (SCT, the duration of an SWS-PS episode). Since TST consists mainly of SWS (mean of 82 percent in this sample of mammals), the correlations between TST and other variables are similar to those for SWS and are not reported separately. Like TST, PS percent is a compound measure involving both SWS and PS; we felt that including these variables might have arbitrary effects on the multivariate analyses. Estimates of SCT are available for only 24 species and do not warrant discussion; however, the strong correlation ($R = .92$) between SCT and brain weight reported by Zepelin and Rechtschaffen (3) was confirmed in this analysis ($R = .89$). The placement of sleep within the 24-hour period (that is, whether the species is nocturnal, diurnal, or polyphasic) is of theoretical interest [W. B. Webb, Percept. Mot. Skills **38**, 1023 (1974)], but few quantitative data are available. The sleep data are primarily from the published literature. In cases in which more than one study was available for a species, the study judged to be more complete for our purposes was chosen.
7. These values came from the following compilations: H. Zepelin and A. Rechtschaffen (2); G. Crile and D. P. Quiring, Ohio J. Sci. **40**, 219 (1940); G. A. Sacher and E. F. Staffeldt, Am. Nat. **108**, 593 (1974); and unpublished values provided by G. A. Sacher.
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13. We tested a variety of stepping sequences since regression analysis is sensitive to the manner in which variables are inserted into the regression equation [see, for example, (12) and N. R. Draper and H. Smith, Applied Regression Analysis (Wiley, New York, 1966)]. Except for the alternatives noted in the text the results given are the most robust. As there is some evidence that SWS and PS are interactive, regression analysis was also made treating SWS as an independent variable on PS and vice versa. For SWS, PS replaced overall danger as a predictor variable, which suggests that overall danger has no significant effect on SWS independent of its association with PS. The results for PS were unchanged.
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15. This interpretation is weakened, however, by the low correlations between gestation time and predation index ($R = .158$) or overall danger ($R = .363$), and by the small partial correlations between these variables ($R = -.02$ and .10, respectively) with the effect of body weight removed. Alternatively, the correlation indicates that large amounts of PS are associated with short gestation times. If the assumption is made that large amounts of PS in the adult are correlated with large amounts in utero [D. Jouvet-Mounier, Ontogenèse des états de vigilance chez quelques mammifères (Tixier, Lyon, 1968)], the correlation is consistent with the notion that PS hastens development of the fetal central nervous system, as proposed by H. P. Roffwarg, J. N. Muzio, and W. C. Dement [Science **152**, 604 (1966)].
16. The raw data for all variables except SWS and the ecological variables were significantly positively skewed; hence, common logarithmic transforms of these variables were used. Univariate and bivariate analysis of distributions revealed that assumptions regarding normality and linearity were adequately met for all variables.
17. Supported by the West Haven Veterans Administration Hospital (MRIS 3185-01) and by National Institute of Mental Health grant MH-05286. We thank F. Snyder for permission to use unpublished data for several African species. An earlier version of these results was given at the Symposium on the Adaptive Value of Sleep, Second International Sleep Research Congress, Edinburgh, 30 June to 4 July 1975.

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