All the values of sleep variables cited by Elgar et al. (1988) for species studied in my laboratory are incorrect, including values based on 24-h recordings (Table I), as is also the case for guinea pigs, *Cavia porcellus* (Jouvet-Mounier & Astic 1966). Other cited values (presumably based on 24-h extrapolations) differ from the original values of Ridgeway et al. (1975) for the grey seal, and from those of Sakaguchi et al. (1979) for the kangaroo rat (Table I).

The origin of many body weight and BMR values are as abstruse. For example, although values for the grey seal are attributed to Elgar & Harvey (1987) and Hayssen & Lacy (1985), this species is not listed in either article. In the case of the marsupial *Lutreolina crassicaudata* a body mass of 812 g and BMR of 0·5 ml O_2/g-h is given in Hayssen & Lacy (1985), whereas Elgar et al. (1988) list a body weight of 1350 g and do not provide a BMR value in their Table I. This species is not listed in Elgar & Harvey (1987). Similarly, although the marsupial *Potorous tridactylous* has entries of 1035 g and 0·455 ml O_2/g-h in Hayssen & Lacy (1985) (no listing in Elgar & Harvey 1987), it is ascribed a body weight of 1600 g without a BMR value in Table I of Elgar et al. (1988). Consequently, values of body weight are misrepresented, and, by not providing published BMR values, these species were excluded from analyses involving BMR, since 'when calculating the genus means we excluded those species with incomplete data' (Elgar et al. 1988, page 1409). Moreover, although mean values of body weight of the animals from which EEG was recorded were reported in some of the primary sources, they were not cited by Elgar et al. (1988), who instead took values from other sources, e.g. *Scalopus aquaticus*: 64–86 g in Allison & Van Twyver (1970); 90 g in Elgar et al. (1988).

In light of the foregoing errors, conclusions drawn by Elgar et al. may have no immediate bearing on the functional implications of previous findings of positive correlations between both total and quiet sleep time with metabolic rate at the level of species (Zepelin & Rechtschaffen 1974; Walker & Berger 1980; Meddis 1983).

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Sources of Variation in Mammalian Sleep

The only possible way to draw general conclusions about sleep is to use data from many different species. In a previous paper (Elgar et al. 1988) we compiled data from diverse sources and, as is inevitable with any comparative study, we had to interpret what different authors meant by their various measures. Berger (1990) has pointed out some errors in the data we used and wonders if our conclusions would hold for a revised data set. We

Table I. Sleep, constitutional and life history variables for 42 species of mammals from 12 orders

Taxa	Body weight (g)	Brain weight (g)	BMR ($cm^3.O_2/h$)	Quiet sleep time (h)	Active sleep time (h)	AS–QS cycle (min)
Marsupialia						
Didelphidae						
Didelphis marsupialis	1329·0	3·9	611·3	13·75	5·64	22·5
Lutreolina crassicaudata	812·0	5·1	406·0	12·86	6·53	—
Phalangeridae						
Trichosurus vulpecula	1982·0	11·4	634·2	12·00	1·68	—
Macropodidae						
Potorous tridactylus	1120·0	—	504·9	10·06	0·62	—
Edentata						
Bradypodidae						
Bradypus tridactylus	3790·0	15·3	686·0	9·33	1·19	38·0
Dasypodidae						
Dasypus novemcinctus	3320·0	8·4	796·8	14·27	3·13	22·8
Priodontes maximus	45 190·0	81·0	3027·7	12·00	6·10	—
Insectivora						
Tenrecidae						
Tenrec ecaudatus	790·0	2·6	260·7	13·26	2·34	—
Erinaceidae						
Erinaceus europeaus	750·0	3·5	337·5	7·20	2·88	17·0
Paraechinus hypomalas	450·0	2·4	112·5	7·50	2·82	—
Soricidae						
Blarina brevicauda	21·0	0·29	52·5	12·60	2·30	7·6
Cryptotis parva	6·4	0·14	44·8	7·70	1·40	8·8
Suncus murinus	52·0	0·33	87·4	10·80	2·00	11·0
Talpidae						
Scalopus aquaticus	48·0	1·2	67·7	6·34	2·11	10·4
Tupaiidae						
Tupaia glis	123·0	3·2	93·5	13·2	2·59	13·9
Chiroptera						
Vespertillionidae						
Eptesicus fuscus	16·9	0·3	20·3	15·80	3·90	7·5
Primates						
Lemuridae						
Lemur macaco	2419·0	25·6	774·1	8·81	0·84	—
Cebidae						
Aotus trivirgatus	1020·0	17·2	459·0	15·15	1·82	—
Cercopithecidae						
Macaca mulatta	5380·0	87·3	1990·6	10·32	1·44	44·5
Pongidae						
Pan troglodytes	36 900·0	410·3	9594·0	9·18	1·62	90·0
Hominidae						
Homo sapiens	70 000·0	1250·0	14 700·0	6·10	1·90	95·8
Carnivora						
Canidae						
Vulpes vulpes	5010·0	48·0	2505·0	7·39	2·40	15·6
Viveridae						
Genetta genetta	1900·0	14·0	—	4·80	1·30	—
Felidae						
Felis silvestris	3260·0	28·4	2314·6	9·48	3·72	20·0
Pinnipedia						
Phocidae						
Phoca caspica	86 000·0	—	—	3·07	0·41	—

Table I. Continued

Taxa	Body weight (g)	Brain weight (g)	BMR ($cm^3.O_2/h$)	Quiet sleep time (h)	Active sleep time (h)	AS–QS cycle (min)
Perissodactyla						
Equidae						
Equus caballas	260 000·0	534·0	65 000·0	2·08	0·78	13·5
Tapiridae						
Tapirus terrestris	160 000·0	250·0	—	5·24	1·00	54·0
Hyracoidea						
Procaviidae						
Dendrohyrax validus	2210·0	12·3	928·2	4·90	0·50	—
Heterohyrax brucei	2000·0	12·0	720·0	5·69	0·91	—
Procavia capensis	2630·0	20·5	1052·0	4·90	0·55	—
Artiodactyla						
Suidae						
Sus scrofa	75 000·0	180·0	8250·0	6·07	1·75	—
Bovidae						
Bos indicus	272 000·0	460·0	46 240·0	3·22	0·75	16·0
Ovis aries	30 000·0	100·0	10 200·0	3·28	0·57	16·5
Rodentia						
Sciuridae						
Spermophilus lateralis	274·0	3·0	123·3	11·76	2·76	—
Spermophilus tridecemlineatus	182·0	4·0	103·7	10·39	3·41	12·5
Muridae						
Dicrostonyx torquatus	47·0	8·9	92·6	12·00	3·19	8·6
Mesocricetus auratus	120·0	1·1	103·2	11·03	3·37	11·6
Mus musculus	20·5	0·4	69·7	9·36	1·92	12·3
Rattus norvegicus	237·0	3·3	312·8	10·67	2·58	8·5
Chinchillidae						
Chinchilla laniger	494·0	5·2	232·2	10·98	1·55	6·5
Aplodontidae						
Aplodontia rufa	630·0	8·1	277·2	11·95	2·45	—
Lagomorpha						
Leporidae						
Oryctolagus cuniculus	1600·0	11·1	—	7·48	1·39	29·0

Sources for sleep variables are given in Elgar et al. (1988); body weight, brain weight and metabolic rate are from McNab (1988), Elgar & Harvey (1987), Hayssen & Lacy (1985), Pagel & Harvey (1988) and Martin & Harvey (1985).

have recalculated all our statistics using the data set revised in the ways suggested by Berger. Our original conclusions stand with one minor exception: although altricial families do have significantly more active sleep time than precocial families, this difference does not remain significant when body weight is controlled for by partial correlation. The data revised according to Berger's criteria are presented in Table I, and the statistics are recalculated below. The data set used to calculate the statistics reported in Elgar et al. (1988) was free from typographical errors.

Nested analysis of variance indicates that the family level is the appropriate level for analysis: more than 80% of the variation was found at the family level or above in all but one variable (active sleep–quiet sleep cycle length, which could not be calculated).

Both total sleep time (TST) and quiet sleep time (QST) correlate significantly and negatively across the 30 families with (log) body weight ($r = -0{\cdot}61$ and $-0{\cdot}63$, respectively, $P < 0{\cdot}01$). This correlation is significant within both the 11 grazing families (TST: $r = -0{\cdot}83$, $P < 0{\cdot}01$; QST: $r = -0{\cdot}85$, $P < 0{\cdot}01$) and the 19 non-grazing families (TST: $r = -0{\cdot}48$, $P < 0{\cdot}05$; QST: $r = -0{\cdot}50$, $P < 0{\cdot}05$). For 26 families TST and QST are correlated with (log) BMR ($r = -0{\cdot}63$ and $-0{\cdot}66$, respectively, $P < 0{\cdot}01$), and there are negative correlations between BMR and both TST and QST after

removing the effects of body weight (partial $r=-0{\cdot}41$ and $-0{\cdot}46$ respectively $P<0{\cdot}05$). Active sleep (AS) has significant negative correlations with (log) body weight and (log) BMR ($r=-0{\cdot}48$, $N=30$, $P<0{\cdot}05$; $r=-0{\cdot}42$, $N=26$, $P<0{\cdot}05$, respectively); these former are non-significant when AS is measured as a percentage of TST.

AS–QS cycle length (the length of time between the onset of successive active sleep episodes) is positively correlated with (log) body weight and (log) BMR ($r=0{\cdot}67$, $N=16$, $P<0{\cdot}01$; $r=0{\cdot}60$, $N=14$, $P<0{\cdot}05$, respectively). However, the relationship between BMR and AS–QS cycle was not significant after controlling for body weight (partial $r=-0{\cdot}27$, $N=14$, NS). AS–QS cycle length is also correlated with (log) brain weight ($r=0{\cdot}74$, $N=16$, $P<0{\cdot}01$), and remains significant even after controlling for body weight and BMR (partial $r=0{\cdot}67$, $N=14$, $P<0{\cdot}05$). But the relationship appears to depend upon the extraordinary encephalization of humans, and is no longer significant after deleting humans from the analysis (partial $r=0{\cdot}56$, $P>0{\cdot}1$). There is a significant association between geographical location and AS–QS cycle length after controlling for body weight ($F=9{\cdot}52$, $N=16$, $P<0{\cdot}005$): tropical families have relatively long AS–QS cycles while temperate families have relatively short AS–QS cycles.

Altricial families have significantly longer AS than precocial families (altricial = 2·2 h, precocial = 1·3 h, $t=2{\cdot}20$, $N=30$, $P<0{\cdot}05$). This difference seems to depend on the fact that precocial species tend to weigh more than altricial species, because the relationship is not significant after controlling for body weight. This is the only conclusion that differs from our original analysis.

The negative correlation between quiet sleep time and metabolic rate, after controlling for body size, differs from the positive correlations reported previously (Zepelin & Rechtschaffen 1974; Walker & Berger 1980; Meddis 1983). Our analysis differed in two ways. First, we controlled for the potentially confounding effect of body size. It is most likely that this procedure is responsible for the difference. Second, we used family means rather than species values in all analyses, because species are not independent and therefore cannot be validly used in significance tests which assume that the data points are independent. Using families greatly reduces the number of degrees of freedom, so our results are most probably conservative. Accordingly, the relationship between AS–QS cycle and brain weight may prove to be significant in larger samples. However, species' data sets are not the appropriate way to increase sample size. Until more independent data become available, we must be cautious about interpreting this and other comparative relationships that depend upon analysing species to obtain significance. We also recognize that taxonomic classifications are subject to revision. For example, assignment of a species to one family rather than another could alter our results. However, incorrect taxonomies will not, on average, systematically bias results. The net effect of error in the taxonomic classifications will be to add noise to the data sets.

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Long-term Paternity Data in Relation to Different Aspects of Rank for Camargue Stallions, *Equus caballus*

Among polygynous mammals, male reproductive success, age and weight are often intercorrelated (Clutton-Brock 1988). The rank of an individual may depend on its age and weight, and in turn determine reproductive success (Dunbar 1988). Mother's rank has also been implicated, by influencing her offspring's early development and adult weight (Clutton-Brock 1988).

How different aspects of social rank affect the reproductive success of males is still unclear and may vary between species. Rank and breeding success of primates are sometimes correlated (review in Silk 1987), and breeding success, rank and mother's rank were intercorrelated for a group of captive rhesus, *Macaca mulatta*, males still in their natal group (Smith & Smith 1988).

A long-term study on Camargue stallions living under semi-natural conditions allowed me to analyse paternities of foals and thus to examine the relationship between reproductive success and a male's own rank, his mother's rank and his weight.

Like other free-living horses (Berger 1986) and zebras, *Equus burchelli* (Klingel 1974), Camargue horses aggregate in small, permanent family-groups (one stallion and one or two mares). Both sexes disperse. Families sometimes have two adult males.

The study herd started in 1974 with 14 horses. They were released in a Camargue pasture of 300 ha, composed of freshwater marshes, salt steppes and halophyte grassland. The number of horses peaked at 94 in 1981, with 11 family groups and one bachelor group. From 1980 on, horses were removed regularly to avoid overgrazing. No supplementary food or veterinary care was given. From 1979 on, all individuals were weighed twice a year. At the same time, blood-samples were taken for paternity tests. All individuals are easily approached and identified and their exact dates of birth are known. Their social behaviour has been monitored regularly.

I consider 11 stallions here (one born in 1972, one in 1973, four in 1974, four in 1976 and one in 1977); they were followed from birth to the age of 11: The others died or were taken out of the herd before this age.

Wells & von Goldschmidt (1979) assessed the dominance hierarchy of the mares, using observations of head threats and bites by one mare, followed by a clear avoidance reaction from another, during contests over food, water or wind-shelter. The dominance hierarchy was stable, linear and based on age. I used the same method to assess the dominance of stallions.

Paternity exclusion tests were based on electrophoresis of a number of proteins at 28 loci (for further procedural details see Scott 1978).

Between 1974 and 1987, 196 foals were born into the herd of which 39 (19·9%) could not be analysed for paternity. Of these, 32 were stillborn or died shortly after birth; their inbreeding-coefficient was not higher than that of the others. The quality of the blood samples of the remaining seven was too poor to be analysed. Only the surviving foals (6 months or older) were considered for the analysis of reproductive success. For 85 (54·1%) of the 157 analysed foals, all but one of the potential fathers could be excluded. For the other 72, the declared father was the stallion in close association with the mother at the date of conception (339 days before birth). Of these foals 80% were born into one-male harems that had already existed for several years. This made it very improbable that outside stallions would be the father. From the analysis on fathers known with certainty, such a case may happen in one out of 49 foals (Duncan et al. 1984).

As the sex-ratio of the herd changed over the study years, stallions of different ages did not have the same possibility of siring foals in each year. To standardize data for each stallion, I calculated the number of 'available' breeding mares for each stallion at each age in the following way. Nearly all the mares in this herd had a foal every year and gestation lasts 11 months. The age at first breeding is taken as 2 for the mares and 4 for the stallions. The number of 'available' breeding mares was thus the ratio of the number of mares 2 or more years old divided by the number of stallions of 4 or more years. So the relative reproductive success of a stallion at a given age was the number of foals produced at that age divided by the number of available breeding mares the year before. I then calculated the total reproductive success up to the age of 11.

Reproductive success varied widely between stallions. The 11 males produced from 0 to 32 foals each (median 10). They started breeding at 3–9 years; seven stallions had their first foal at the age of 5. The end of the reproductive lifespan could not be established. The oldest stallion of the herd was 18 in 1990 and still fathered foals.