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Phylogenetics and the correlates of mammalian sleep: A reappraisal

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KEYWORDS

Comparative approach;
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Mammals;
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Summary The correlates of mammalian sleep have been investigated previously in at least eight comparative studies in an effort to illuminate the functions of sleep. However, all of these univariate analyses treated each species, or taxonomic Family, as a statistically independent unit, which is invalid due to the phylogenetic relationships among species. Here, we reassess these influential correlates of mammalian sleep using the formal phylogenetic framework of independent contrasts. After controlling for phylogeny using this procedure, the interpretation of many of the correlates changed. For instance, and contrary to previous studies, we found interspecific support for a neurophysiological role for rapid-eye-movement sleep, such as memory consolidation. Also in contrast to previous studies, we did not find comparative support for an energy conservation function for slow-wave sleep. Thus, the incorporation of a phylogenetic control into comparative analyses of sleep yields meaningful differences that affect our understanding of why we sleep.

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Introduction

Great interspecific variation exists in the time mammals spend in slow-wave sleep (SWS) and

rapid-eye-movement (REM) sleep.¹ For decades, researchers have tried to shed light on the functions of sleep by identifying the factors responsible for maintaining such variation in the structure of sleep.^{1–11} For example, Zepelin and Rechtschaffen² found that species with a higher per-gram basal metabolic rate (BMR) engaged in more SWS, supporting an energy conservation role for this sleep state.¹² Zepelin et al.¹⁰ found that species with greater encephalization (a potential measure of interspecific cognitive abilities^{13,14}) allocated less time asleep to REM sleep, thus challenging a neurophysiological role, such as memory consolidation, for REM sleep.^{9,10,15}

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However, all of these univariate comparative studies treated each species^{2-4,8-11} (Figure 1a), or taxonomic Family^{5,6} (the nodes in Figure 1b), as a statistically independent unit, thus violating the assumption of independence required by any statistical analysis, including correlation.¹⁶ Characteristics of species, especially closely related species, are inherently non-independent due to their recently shared evolutionary history.¹⁷ That is, two species that share a recent common ancestor will be more similar to one another than to a third, more distantly related species (in part) because the former share that recent common ancestor (e.g., Figure 1c). Consequently, relationships among measures of sleep architecture and factors that influence sleep identified by previous studies were confounded by such phylogenetic effects and therefore may not be robust to reanalysis using modern phylogenetically based comparative techniques.¹⁷⁻²⁰

The use of a phylogenetic control in comparative studies is not new.¹⁷⁻²⁰ Such procedures have long been used as a standard in diverse subdisciplines of biology, including neuroscience,²¹ but the use of these methods has been largely side-stepped in comparative sleep research. Recently, we used phylogenetically controlled data to assess comparative support for some hypotheses for the functions of sleep.¹ However, Lesku et al.¹ focused on multivariate techniques, thus a comparison of the correlates of mammalian sleep per se using non-phylogenetically controlled (raw) and phylogenetically controlled data was outside the scope of that study. We note further that Elgar et al.^{5,6} recognized the problem of phylogenetic non-independence. Elgar et al.^{5,6} determined the taxonomic level at which the most variation in sleep existed

(e.g., Family) and then averaged species-values to that taxonomic level. Unlike previous studies, Elgar et al.^{5,6} found that the relationships between REM sleep and body mass, brain mass, and BMR were non-significant. However, the phylogenetic control used by Elgar et al.^{5,6} weighted all taxonomic Families equally and has since been replaced by more rigorous procedures, such as independent contrasts, that take the degree of relatedness among species into consideration.¹⁷⁻²⁰

Here, inspired by the renewed interest in the correlates of sleep,^{8-11,15} we reassess these influential relationships using the formal phylogenetic framework of independent contrasts¹⁸ with a greatly expanded data set based on electrophysiological data for 83 species (Table 1). Overall, we show that controlling for shared evolutionary history among species causes several of the previously identified correlates of mammalian sleep to change in a manner that influences our understanding of how long and why mammals sleep.

Building the comparative data set

‘Sleep’ was expressed as the duration of time spent in SWS or REM sleep over a 24-hr day, and the percentage of total sleep time allocated to REM sleep (%REM sleep). Sleep data were included only from studies that quantified the time spent in SWS and REM sleep based upon electrophysiology of adult mammals (Table 1, see Lesku et al.¹ for details). We note that although the intensity or depth of SWS based on electroencephalogram spectral power density²² may be the more appropriate measure for this sleep state, SWS intensity has only rarely been reported.

We considered the four ‘traditional’ constitutive variables used in previous studies: body mass, brain mass, BMR, and gestation period. Values for all constitutive traits were taken from the primary study when available (as per Berger⁷) or another published source (e.g.,^{97,98}). Brain mass of the Mexican volcano mouse (*Neotomodon alstoni*) was provided by A. Castro and I. Villalpando (pers. comm.). Using skulls from the Field Museum (Chicago, IL, USA), we estimated brain mass from endocranial volume for four species (Siberian musk deer, *Moschus moschiferus*; yellow-bellied marmot, *Marmota flaviventris*; Heermann’s kangaroo rat, *Dipodomys heermanni*; Djungarian hamster, *Phodopus sungorus*) as per Iwaniuk and Nelson.⁹⁹ BMRs for 27 of the 83 species were unavailable; thus correlations involving BMR are based on data for

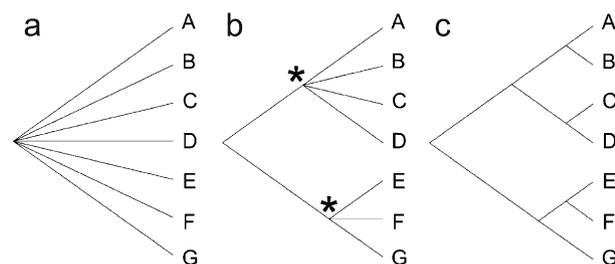


Figure 1 Three phylogenetic trees of increasing resolution. The letters A–G represent species: (a) the tree implicitly used in studies that treated each species as an independent unit^{2-4,8-11}; (b) the tree used in Elgar et al.^{5,6} where species data were averaged to Family (e.g., the nodes, which are represented here by asterices); and (c) the phylogenetic tree similar to that used in Lesku et al.¹ where the evolutionary histories among species are estimated based on molecular data.

Table 1 Data set of sleep, constitutive, and ecological variables for 83 mammalian species.

Order	Family	Species	Common name	SWS time (h)	REM sleep time (h)	Body mass (g)	Brain mass (g)	BMR (cm ³ O ₂ h ⁻¹)	Gestation period (days)	Sleep exposure index	References for sleep values
Didelphimorphia	Didelphidae	<i>Didelphis marsupialis</i>	Southern opossum	13.75	5.65	1600	3.90	611.30	13.2	2.25	van Twyver and Allison ²³
Didelphimorphia	Didelphidae	<i>Didelphis virginiana</i>	Virginia opossum	8.98	7.34	2636	7.55	869.88	12.6	2.25	Walker and Berger ²⁴
Didelphimorphia	Didelphidae	<i>Lutreolina crassicaudata</i>	Lutrine opossum	12.86	6.53	812	5.10	406.00	14.0	2.67	Affanni ²⁵ (Elgar et al. ⁶)
Diprotodontia	Phalangeridae	<i>Trichosurus vulpecula</i>	Brush-tail possum	12.00	1.68	1982	11.40	634.20	18.0	1.50	LoPresti and McGinty ²⁶ (Elgar et al. ⁶)
Diprotodontia	Potoroidae	<i>Potorous tridactylus</i>	Long-nosed potoroo	10.06	0.62	1120	12.00	504.00	33.6	2.00	Astic et al. ²⁷ (Elgar et al. ⁶)
Xenarthra	Bradypodidae	<i>Bradypus tridactylus</i>	Pale-throated three-toed sloth	9.34	1.19	3790	15.30	686.00	106.0	4.00	de Moura Filho et al. ²⁸
Xenarthra	Dasypodidae	<i>Chaetophractus villosus</i>	Large hairy armadillo	15.94	4.48	3500	16.40	623.00	67.5	1.00	Affanni et al. ²⁹
Xenarthra	Dasypodidae	<i>Dasypus novemcinctus</i>	Nine-banded armadillo	14.41	3.56	3320	8.40	796.80	134.5	1.00	Prudom and Klemm ³⁰ ; van Twyver and Allison ³¹
Xenarthra	Dasypodidae	<i>Priodontes maximus</i>	Giant armadillo	12.00	6.10	45190	81.00	3027.70	120.0	1.00	Affanni ²⁵ (Elgar et al. ⁶)
Insectivora	Tenrecidae	<i>Tenrec ecaudatus</i>	Common tenrec	13.26	2.34	790	2.60	260.70	59.3	1.50	Snyder et al. ³² (Elgar et al. ⁶)
Insectivora	Erinaceidae	<i>Erinaceus europaeus</i>	Western European hedgehog	7.20	2.88	750	3.50	337.50	35.5	2.33	Snyder et al. ³² (Elgar et al. ⁶); Toutain and Ruckebusch ³³ (Elgar et al. ⁶)
Insectivora	Erinaceidae	<i>Paraechinus hypomelas</i>	Brandt's hedgehog	7.50	2.82	450	2.40	112.50	37.0	1.00	Tauber et al. ³⁴ (Elgar et al. ⁶)
Insectivora	Soricidae	<i>Blarina brevicauda</i>	Northern short-tailed shrew	12.60	2.30	21	0.29	52.50	17.0	1.00	Allison et al. ³⁵ (Elgar et al. ⁶)
Insectivora	Soricidae	<i>Cryptotis parva</i>	Least shrew	7.70	1.40	6	0.14	44.80	18.0	1.33	Allison et al. ³⁵ (Elgar et al. ⁶)
Insectivora	Soricidae	<i>Suncus murinus</i>	House shrew	10.80	2.00	52	0.33	87.40	30.1	1.00	Allison et al. ³⁵ (Elgar et al. ⁶)
Insectivora	Talpidae	<i>Condylura cristata</i>	Star-nosed mole	8.15	2.17	70	1.00	157.50	45.0	1.00	Allison and van Twyver ³⁶ (Elgar et al. ⁵)

Table 1 (continued)

Order	Family	Species	Common name	SWS time (h)	REM sleep time (h)	Body mass (g)	Brain mass (g)	BMR (cm ³ O ₂ h ⁻¹)	Gestation period (days)	Sleep exposure index	References for sleep values
Insectivora	Talpidae	<i>Scalopus aquaticus</i>	Eastern mole	6.34	2.11	75	1.16	67.70	39.9	1.00	Allison and van Twyver ³⁶ (Elgar et al. ⁶)
Scandentia	Tupaiaidae	<i>Tupaia glis</i>	Common tree shrew	13.20	2.59	123	3.20	93.50	45.2	2.00	Berger and Walker ³⁷ (Elgar et al. ⁶)
Chiroptera	Vespertilionidae	<i>Eptesicus fuscus</i>	Big brown bat	15.80	3.90	17	0.30	20.30	47.5	2.00	Zepelin and Rechtschaffen ²
Chiroptera	Vespertilionidae	<i>Myotis lucifugus</i>	Little brown bat	17.93	1.99	10	0.30	48.30	70.0	2.00	Brebbia and Pyne ³⁸ (Elgar et al. ⁵)
Primates	Cheirogaleidae	<i>Microcebus murinus</i>	Gray mouse lemur	12.94	1.37	60	1.82	—	60.1	2.50	Barre and Petter-Rousseaux ³⁹
Primates	Lemuridae	<i>Eulemur macaco</i>	Black lemur	8.81	0.84	2419	25.60	774.10	132.5	3.00	Balzamo et al. ⁴⁰ (Elgar et al. ⁶)
Primates	Lemuridae	<i>Eulemur mongoz</i>	Mongoose lemur	11.52	0.36	1800	21.60	—	128.0	3.00	Balzamo et al. ⁴⁰ (Elgar et al. ⁵)
Primates	Galagidae	<i>Galago senegalensis</i>	Senegal galago	6.93	0.87	212	4.80	—	125.9	2.50	Bert et al. ⁴¹ (Elgar et al. ⁵)
Primates	Callitrichidae	<i>Callithrix jacchus</i>	Common marmoset	7.89	1.60	410	7.70	328.00	142.9	2.00	Crofts et al. ⁴²
Primates	Cebidae	<i>Aotus trivirgatus</i>	Northern night monkey	15.15	1.82	1020	17.20	459.00	139.0	1.00	Perachio ⁴³ (Elgar et al. ⁶)
Primates	Cebidae	<i>Saimiri sciureus</i>	Common squirrel monkey	8.10	1.03	988	22.40	489.70	167.0	3.00	Wexler and Moore-Ede ⁴⁴ ; Edgar ⁴⁵
Primates	Cercopithecidae	<i>Chlorocebus aethiops</i>	Vervet monkey	9.74	0.60	4173	64.20	—	170.8	4.00	Bert and Pegram ⁴⁶ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Erythrocebus patas</i>	Patas monkey	9.99	0.86	5600	106.60	—	167.8	4.00	Bert and Pegram ⁴⁶ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Macaca arctoides</i>	Stump-tailed macaque	8.00	1.52	9667	100.70	—	180.2	4.00	Leinonen and Stenberg ⁴⁷
Primates	Cercopithecidae	<i>Macaca mulatta</i>	Rhesus macaque	7.97	0.98	11900	87.30	1990.60	163.7	4.00	Balzamo et al. ⁴⁸
Primates	Cercopithecidae	<i>Macaca nemestrina</i>	Pig-tail macaque	8.54	1.06	7800	114.00	—	171.1	4.00	Reite et al. ⁴⁹ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Macaca radiata</i>	Bonnet macaque	8.12	1.05	3700	76.80	—	164.0	4.00	Bert et al. ⁵⁰ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Macaca sylvanus</i>		10.68	1.07	8050	95.55	—	164.6	4.00	Gonzalez et al. ⁵¹

Primates	Cercopithecidae	<i>Papio anubis</i>	Barbary macaque Olive baboon	8.38	1.39	9500	175.10	2850.00	184.0	4.00	Balzamo and Bert ⁵² (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Papio cynocephalus</i>	Yellow baboon	9.11	0.78	16630	169.10	–	175.0	4.00	Balzamo ⁵³ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Papio hamadryas</i>	Hamadryas baboon	8.58	1.26	14350	156.00	–	178.6	2.00	Bert ⁵⁴ (Elgar et al. ⁵)
Primates	Cercopithecidae	<i>Papio papio</i>	Guinea baboon	8.44	0.54	17600	192.00	2554.30	175.0	4.00	Bert ⁵⁴ (Elgar et al. ⁵); Bert et al. ⁵⁵ (Elgar et al. ⁵)
Primates	Hominidae	<i>Homo sapiens</i>	Human	6.10	1.90	62000	1320.00	14700.00	280.1	1.00	Meddis ⁴
Primates	Hominidae	<i>Pan troglodytes</i>	Chimpanzee	9.18	1.62	36900	410.30	9594.00	223.8	4.00	McNew et al. ⁵⁶ (Elgar et al. ⁶); Balzamo et al. ⁵⁷ (Elgar et al. ⁶)
Carnivora	Canidae	<i>Canis familiaris</i>	Domestic dog	7.08	1.55	14000	70.00	–	62.0	2.00	Copley et al. ⁵⁸ ; Lucas et al. ⁵⁹
Carnivora	Canidae	<i>Vulpes vulpes</i>	Red fox	7.39	2.40	5010	48.00	2505.00	52.0	1.00	Dallaire and Ruckebusch ⁶⁰ (Elgar et al. ⁶)
Carnivora	Mustelidae	<i>Mustela putorius</i>	Domestic ferret	8.64	5.86	145	4.56	–	41.2	1.33	Marks and Shaffery ⁶¹
Carnivora	Viverridae	<i>Genetta genetta</i>	Common genet	4.80	1.30	1900	14.00	–	77.8	1.33	Meddis ⁴
Carnivora	Felidae	<i>Felis silvestris</i>	Domestic cat	10.01	3.22	3260	28.40	2314.60	63.9	1.50	Ursin ⁶²
Carnivora	Otariidae	<i>Arctocephalus pusillus</i>	Cape fur seal	6.58	1.10	70000	369.38	–	368.5	7.00	Lyamin and Chetyrbok ⁶³
Carnivora	Otariidae	<i>Callorhinus ursinus</i>	Northern fur seal	6.39	0.91	22000	339.88	–	361.8	7.00	Mukhametov et al. ⁶⁴ ; Mukhametov et al. ⁶⁵
Carnivora	Otariidae	<i>Otaria byronia</i>	Southern sea lion	3.60	2.33	32667	520.83	–	365.0	7.00	Lyamin et al. ⁶⁶
Carnivora	Phocidae	<i>Halichoerus grypus</i>	Grey seal	4.70	1.50	85000	325.00	–	355.6	7.00	Ridgway et al. ⁶⁷
Carnivora	Phocidae	<i>Phoca caspica</i>	Caspian seal	3.07	0.41	50000	153.93	–	330.0	7.00	Mukhametov et al. ⁶⁸
Perissodactyla	Equidae	<i>Equus caballus</i>	Horse	2.09	0.79	260000	534.00	65000.00	337.0	5.00	Ruckebusch ⁶⁹
Hyracoidea	Procaviidae	<i>Dendrohyrax validus</i>	Eastern tree hyrax	4.39	0.50	2210	12.30	928.20	228.6	2.00	Snyder ⁷⁰
Hyracoidea	Procaviidae	<i>Heterohyrax brucei</i>	Yellow-spotted hyrax	4.78	0.91	2000	12.00	720.00	228.8	1.00	Snyder ⁷⁰
Hyracoidea	Procaviidae	<i>Procavia capensis</i>	Rock hyrax	4.34	0.55	2630	20.50	1052.00	222.4	1.00	Snyder ⁷⁰
Artiodactyla	Suidae	<i>Sus scrofa</i>	Pig	6.40	2.63	75000	180.00	8250.00	117.0	5.00	Robert and Dallaire ⁷¹
Artiodactyla	Moschidae	<i>Moschus moschiferus</i>	Siberian musk deer	9.50	0.74	12500	47.92	–	167.3	5.00	Sokolov et al. ⁷²
Artiodactyla	Bovidae	<i>Bos taurus</i>	Cow	3.22	0.75	272000	460.00	46240.00	280.7	5.00	Ruckebusch ⁶⁹
Artiodactyla	Bovidae	<i>Capra aegagrus</i>	Goat	4.69	0.71	29000	115.00	6840.00	163.9	5.00	Bell ⁷³ (Elgar et al. ⁵)

Table 1 (continued)

Order	Family	Species	Common name	SWS time (h)	REM sleep time (h)	Body mass (g)	Brain mass (g)	BMR (cm ³ O ₂ h ⁻¹)	Gestation period (days)	Sleep exposure index	References for sleep values
Artiodactyla	Bovidae	<i>Ovis aries</i>	Sheep	3.28	0.57	30000	100.00	10200.00	146.3	5.00	Ruckebusch ⁶⁹
Rodentia	Aplodontidae	<i>Aplodontia rufa</i>	Mountain beaver	11.95	2.45	630	8.10	277.20	29.7	1.00	Snyder et al. ³² (Elgar et al. ⁶)
Rodentia	Sciuridae	<i>Tamias sibiricus</i>	Siberian chipmunk	9.26	2.94	113	2.08	—	33.6	1.00	Dijk and Daan ⁷⁴
Rodentia	Sciuridae	<i>Marmota flaviventris</i>	Yellow-bellied marmot	15.61	1.81	5000	11.63	963.33	30.0	1.00	Miller and South ⁷⁵ (Elgar et al. ⁵)
Rodentia	Sciuridae	<i>Spermophilus beldingi</i>	Belding's ground squirrel	12.83	3.01	293	3.87	123.06	26.8	1.00	Walker et al. ⁷⁶ (Elgar et al. ⁵)
Rodentia	Sciuridae	<i>Spermophilus lateralis</i>	Golden-mantled ground squirrel	11.76	2.76	274	3.00	123.30	29.8	1.00	Walker et al. ⁷⁶ (Elgar et al. ⁶); Haskell et al. ⁷⁷ (Elgar et al. ⁶)
Rodentia	Sciuridae	<i>Spermophilus parryi</i>	Arctic ground squirrel	12.70	3.38	908	5.70	—	25.0	1.00	Chepkasov ⁷⁸ (Elgar et al. ⁵)
Rodentia	Sciuridae	<i>Spermophilus tridecemlineatus</i>	Thirteen-lined ground squirrel	10.39	3.41	182	4.00	103.70	27.5	1.00	van Twyver ⁷⁹
Rodentia	Heteromyidae	<i>Dipodomys heermanni</i>	Heermann's kangaroo rat	13.28	2.72	60	1.15	—	30.7	1.00	Sakaguchi et al. ⁸⁰ (Elgar et al. ⁵)
Rodentia	Heteromyidae	<i>Perognathus longimembris</i>	Little pocket mouse	16.91	3.15	8	0.93	9.10	21.8	1.00	Walker et al. ⁸¹ (Elgar et al. ⁵)
Rodentia	Muridae	<i>Cricetomys gambianus</i>	African giant pouched rat	6.30	2.00	1000	6.60	—	34.4	1.33	Meddis ⁴
Rodentia	Muridae	<i>Dicrostonyx torquatus</i>	Collared lemming	12.00	3.19	47	8.90	92.60	18.0	1.00	Karmanova et al. ⁸² (Elgar et al. ⁶)
Rodentia	Muridae	<i>Meriones unguiculatus</i>	Mongolian jird	10.95	2.18	70	1.00	98.00	25.6	1.00	Susic and Masirevic ⁸³
Rodentia	Muridae	<i>Mesocricetus auratus</i>	Golden hamster	11.47	3.51	120	1.10	103.20	16.0	1.00	van Twyver ⁷⁹ ; Tobler and Jaggi ⁸⁴
Rodentia	Muridae	<i>Mus musculus</i>	House mouse	11.89	1.26	21	0.40	69.70	21.2	1.33	van Twyver ⁷⁹
Rodentia	Muridae	<i>Neotomodon alstoni</i>	Mexican volcano mouse	15.49	1.81	80	1.05	-	27.3	1.00	Ayala-Guerrero et al. ⁸⁵
Rodentia	Muridae	<i>Phodopus sungorus</i>	Djungarian hamster	12.23	2.07	36	0.50	73.44	19.9	1.00	Deboer et al. ⁸⁶⁻⁸⁹
Rodentia	Muridae	<i>Rattus norvegicus</i>	Norway rat	10.66	2.58	237	3.30	312.80	21.8	2.33	van Twyver ⁷⁹
Rodentia	Muridae			9.82	1.48	132	1.20	145.20	26.8	2.33	

Non-phylogenetic analysis

Here, correlations between sleep variables and constitutive and ecological variables are based on non-phylogenetically controlled (raw) data as in all existing comparative studies of sleep (except Elgar et al.^{5,6} and Lesku et al.¹). That is, correlations are based directly on the data presented in Table 1. Most variables, however, were first log transformed to meet the assumption of normality; %REM sleep was arcsin square root transformed. We calculated Pearson's product moment correlation coefficients between pairs of variables in SPSS 15.0.¹⁰¹ These raw data correlations are not statistically valid, but are included as a comparison with both the phylogenetically controlled correlations and previously published work. Per comparison alphas were adjusted based on the sequential Bonferroni correction for multiple comparisons.¹⁰²

Phylogenetic analysis

To transform our comparative data set into one of statistically independent data, we constructed a phylogenetic tree that depicts evolutionary relationships among species. Our phylogenetic tree for the species in Table 1 (Figure 2) is an amalgam based on the Order-level tree of Murphy et al.¹⁰³ derived from the molecular analysis of 9779 basepairs from 15 nuclear and three mtDNA genes. Lower-level trees supplied the within-Order and within-Family clade topology (see Lesku et al.¹ for details). Branch lengths could not be determined and were thus set to one.^{19,20} Normalized raw variables were entered into COMPARE 4.6b,¹⁰⁴ a software package that uses the evolutionary relationships among taxa (e.g., Figure 2) to transform comparative data into a set of independent contrasts.¹⁸ Independent contrasts are calculated as the difference in values between sister taxa; this difference is assumed to reflect phenotypic changes that occurred since the two sister taxa diverged.¹⁸ Contrasts are calculated for $N-1$ sister-taxa comparisons from the $N = 83$ tip species to deep nodes. The resulting independent contrasts were then used for the phylogenetically controlled analysis. We confirmed that contrasts were effectively standardized by examining plots of contrasts vs. standard deviation, which showed slopes of approximately zero.^{19,20} Since BMRs were available for only 56 species, we modified our phylogenetic tree accordingly and ran a separate analysis to obtain the standardized phylogenetically controlled independent contrasts for this variable. Phylogenetically controlled residual (relative) values

of brain mass, BMR, and gestation period were obtained from regressions of independent contrasts with body mass contrasts.

Pearson's correlation coefficients were calculated between pairs of variables using the independent contrast data forced through the origin.²⁰ Per comparison alphas were adjusted based on the sequential Bonferroni correction for multiple comparisons.¹⁰² The phylogenetically controlled correlations presented here are qualitatively very similar to those relationships identified in Lesku et al.¹ Minor differences exist because variance is partitioned among more variables in a multivariate analysis than in simple correlation. We note that the interpretation of an independent contrast-based correlation differs somewhat from one based on the raw data. A contrast-based correlation reflects the correlated evolution between two traits along the evolutionary history of the group of interest.¹⁸ A raw data-based correlation reflects a change in one variable for a given change in another. For example, a significant negative (raw data) correlation between body mass and SWS time would suggest that an increase in body mass is associated with a reduction in the time spent in SWS in extant species, whereas a significant negative correlation between contrasts of body mass and contrasts of SWS time would suggest that evolutionary increases in body mass are associated with evolutionary reductions in the time spent in SWS over the evolution of mammals.

The phylogenetically controlled correlates of mammalian sleep

The need for a phylogenetic control is apparent in Figure 3. In Figure 3a, the strong negative (raw data) relationship between the time spent in REM sleep and brain mass identified in previous studies is apparent. However, the relationship between REM sleep and brain mass within the two highlighted (well-represented) Orders, Rodentia and Primates, is non-significant ($r = 0.164$, $N = 23$, $P = 0.453$ and $r = 0.109$, $N = 20$, $P = 0.646$, respectively). These two Orders also show little overlap with one another and are statistically clumped with respect to themselves (discriminant function analysis: Wilks' lambda = 0.272, approximate $F_{2,40} = 53.617$, $P < 0.001$). This clumped, non-independent pattern, typical of non-phylogenetically controlled data, reflects the fact that closely related species (e.g., species within Rodentia) are often more similar to one another than they are to more distantly related species (e.g., species within Primates). In Figure 3b,

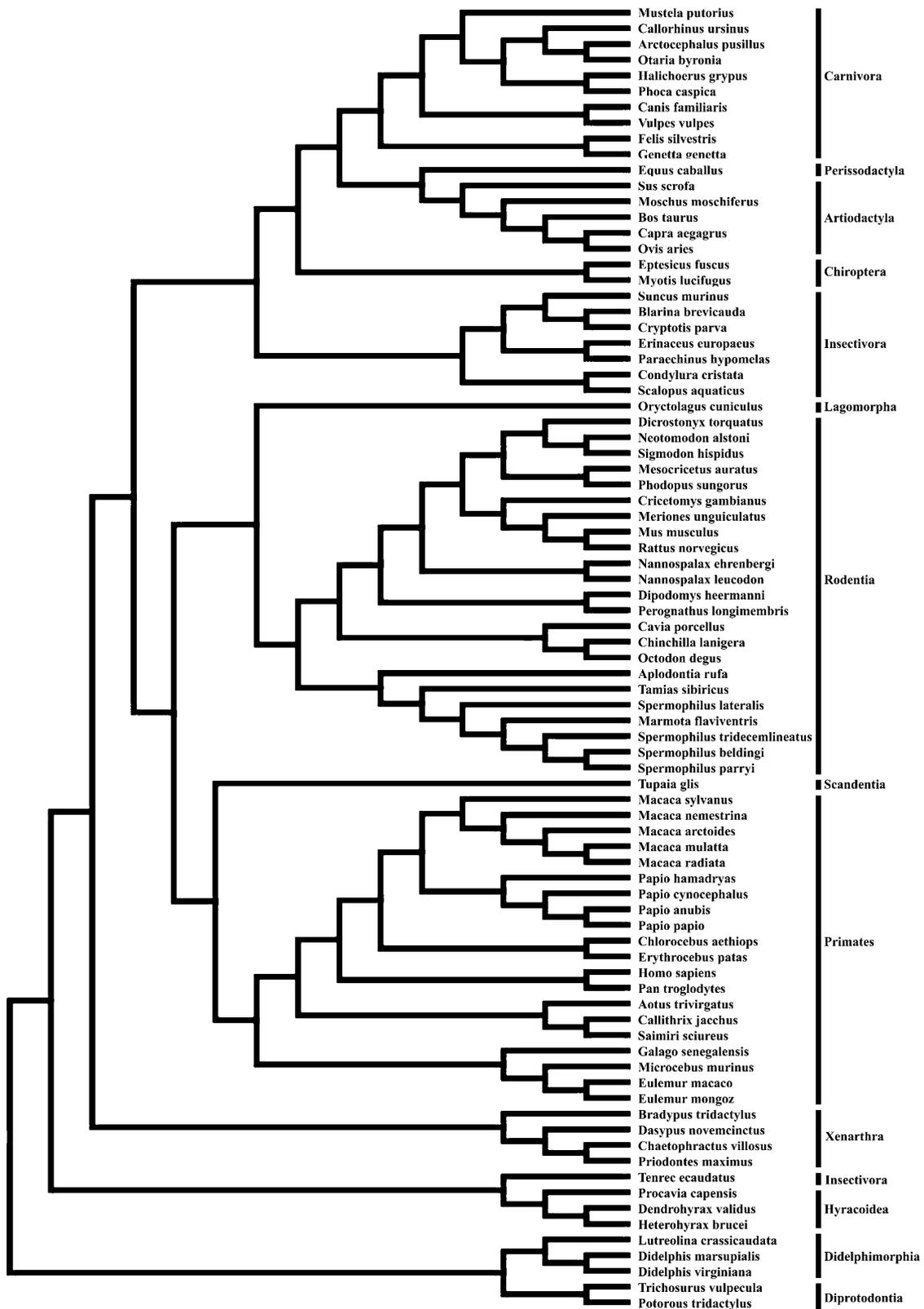


Figure 2 Phylogenetic tree depicting the evolutionary relatedness among the 83 mammalian species in our comparative data set.

however, phylogenetically controlled data generated within the same two Orders show much more overlap with one another (Wilks' lambda = 0.951, approximate $F_{2,38} = 0.982$, $P = 0.384$), indicative of a phylogenetic control. Similarly, taxonomic membership is predicted well in Figure 3a (96% and 85% of all rodents and primates classified correctly, respectively), and poorly in Figure 3b (59% and 58% of all rodents and primates classified correctly, respectively) as expected when a phylogenetic control is applied. Consequently in Figure 3b, the overall relationship between REM sleep and brain mass is now non-significant and (as observed in Figure 3a) is the same relationship within rodents ($r = 0.366$, $N = 22$, $P = 0.094$) and primates ($r = -0.084$, $N = 19$, $P = 0.731$). Another example of a possible effect of controlling for phylogeny is shown in Figure 3. In Figure 3c, the relationship between residual brain mass and %REM sleep is

positive across rodents ($r = 0.309$, $N = 23$, $P = 0.152$) and primates ($r = 0.494$, $N = 20$, $P = 0.027$), but the overall relationship across all taxa is negative (Figure 3c) due to the clumped, non-independent pattern discussed above. However, once phylogenetic relatedness has been controlled, the relationship within rodents ($r = 0.416$, $N = 22$, $P = 0.054$) and primates ($r = 0.354$, $N = 19$, $P = 0.137$) remains positive, but the overall relationship across all taxa is now positive as well (Figure 3d).

After controlling for shared evolutionary history among species, many of the significant raw data correlations became non-significant (compare the raw data-based correlations in Table 2a with the contrast-based correlations in Table 2b). The magnitude of 62% of all correlations decreased to some extent because additional variance was explained by phylogenetic relatedness; the abso-

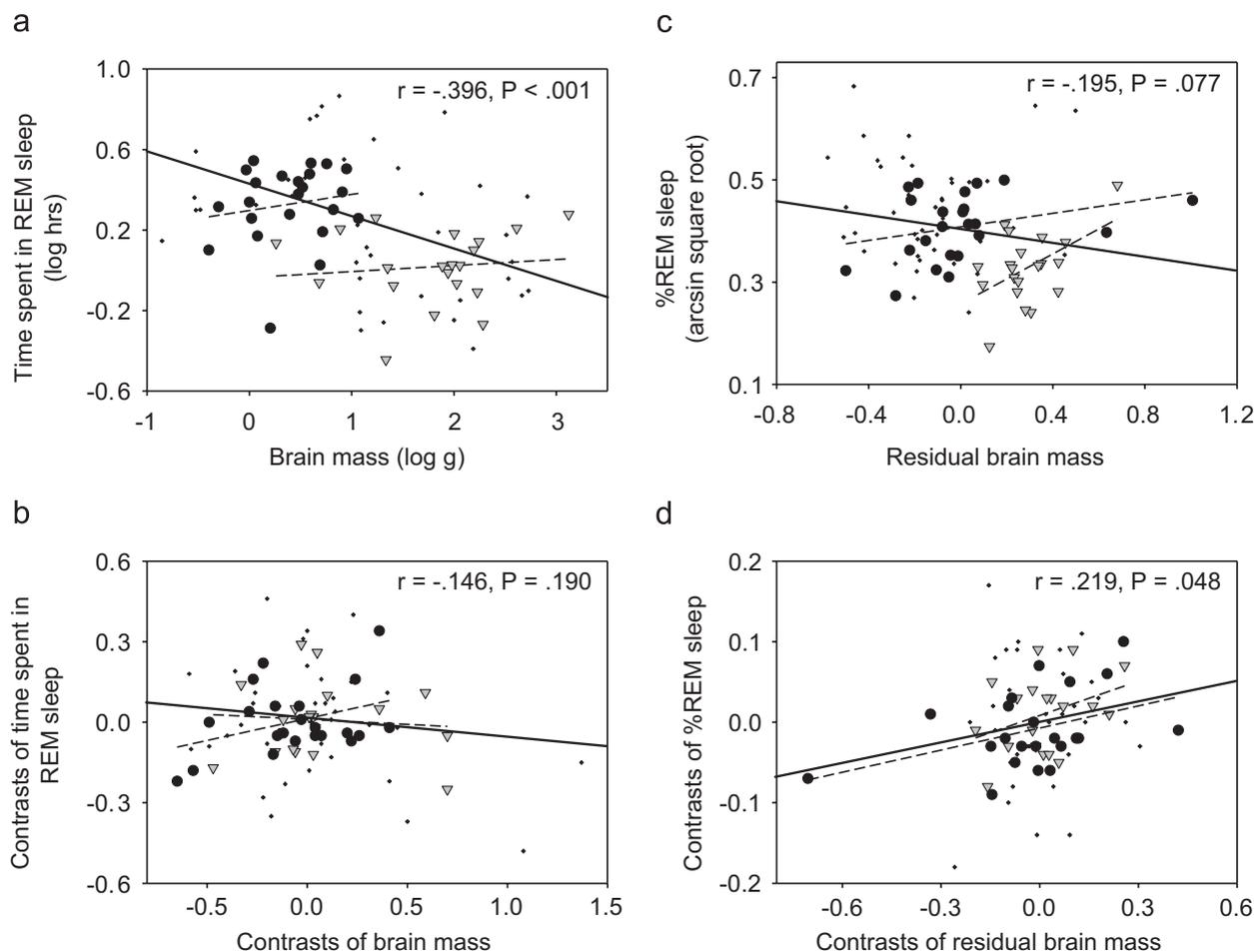


Figure 3 Left: scatterplots of brain mass vs. REM sleep time based on (a) raw data and (b) phylogenetically controlled independent contrast data. Right: scatterplots of residual brain mass vs. %REM sleep based on (c) raw data and (d) independent contrast data. The two best-represented Orders in our data set, Rodentia and Primates, are highlighted as solid circles and gray triangles, respectively. Data points from all other taxa/contrasts are represented by plus (+) symbols. The regression line based on data for all taxa is shown as a solid black line, and the regression lines for Rodentia and Primates are shown as dashed lines within the data range of each taxonomic group.

lute range of change in effect size between analyses was 0.001–0.414 (compare Table 2a,b). We note also that the relationship between residual brain mass and %REM sleep was marginally significant and negative in the raw data analysis, but changed sign after taking phylogenetic effects into account (compare Table 2a,b, see also Figure 3c,d).

Table 2b reflects the most statistically defensible correlations between sleep and constitutive and ecological variables (see Lesku et al.¹ for a multivariate approach). The general correlational trends can be summarized as follows. Increases in body mass, brain mass, absolute BMR, and gestation period are associated with decreases in the time spent in SWS across evolutionary time. Increases in gestation period and “precociality”, as indicated by residual gestation period, are associated with decreases in the time spent in REM sleep. We identified a tendency for species sleeping in riskier environments to also engage in less REM sleep, and evolutionary increases in encephalization to be associated with increases in the proportion of sleep time allocated to REM sleep; these relationships were significant in our previous study in the context of our phylogenetically controlled multivariate models.¹ In fact, in these previous models, the non-significant negative relationship between residual BMR and SWS time identified above was negative, but significant. Also, we previously found that species sleeping in riskier environments and species more precocial at birth allocated a lower proportion of total sleep time to REM sleep than those sleeping at safer locations and more altricial species, respectively.¹ Our multivariate models acknowledged the complexity and likely multifunctional nature of sleep by quantifying the relationships among the variables in Table 1 simultaneously, and thus represent a more comprehensive view of sleep than the correlations offered above, which serve to illustrate the importance of a phylogenetic control in comparative sleep research.

Evolutionary relationships and the functions of sleep

These corrections to the correlates of mammalian sleep may relate directly to the functions of sleep.^{1,9,15} For instance, our finding of correlated evolution between increases in encephalization and increases in the proportion of time asleep devoted to REM sleep would seem to support a neurophysiological role for REM sleep.¹ This positive relationship is consistent with experimental data implicating REM sleep in memory consolidation.¹⁰⁵

REM sleep might also be important for early brain development^{106,107} in part because species more altricial at birth (i.e., newborns that are more dependent on their parents) engage in more REM sleep as adults than species that are more developed at birth (i.e., precocial species). This interpretation may, at first, seem unlikely as the sleep times in Table 1 are derived from adults; however, %REM sleep in altricial species as adults predicts %REM sleep in altricial young.¹⁰⁸ Regardless, the specific mechanism underlying this relationship remains enigmatic.⁸ The lack of a significant positive relationship between residual brain mass and SWS does not necessarily preclude a functional role for SWS in memory consolidation, as suggested by experimental studies.^{109,110} The intensity of SWS based on electroencephalogram spectral power density²² may be the more appropriate measure for this sleep state. Unfortunately, SWS intensity was rarely reported in the studies listed in Table 1. The incorporation of intensity measurements (in addition to time) into future comparative studies represents an important avenue of research.

Under the energy conservation hypothesis,¹² one might expect that species with higher relative BMRs would engage in more SWS to conserve energy. Several previous studies did identify such a relationship^{2,10}; however, in our raw data and contrast-based analyses (above) we found the relative BMR-SWS relationships to be *negative* (see also Lesku et al.¹). This stark inconsistency is actually due to methodological differences in the statistical control of body mass. Zepelin and Rechtschaffen² and Zepelin et al.¹⁰ used per-gram BMR (i.e., BMR/body mass), whereas we used the residuals of BMR from a BMR vs. body mass regression (see also Elgar et al.^{5,6}). The latter approach is the more effective statistical control of body mass as BMR does not vary as a constant proportion of body mass.^{111–113} Hence, we believe that the negative relationships between residual BMR and SWS time and REM sleep time are more accurate. These negative relationships may reflect increased foraging demands associated with increased residual BMR and hence less time available for sleep⁵ or that the restorative neurophysiological processes occurring during SWS occur faster with higher residual BMR, such that these processes are accomplished quicker and thus less SWS is required.¹

Conclusions

Results of previous comparative studies of sleep have influenced the development of several hypotheses for the functions of sleep.⁹ Our analyses

Table 2 Correlation coefficients between sleep and constitutive and ecological variables based on (a) raw data ($N = 83$ species for all correlations except for basal metabolic rate (BMR)-related relationships where $N = 56$ species) and (b) contrast data ($N = N_{\text{raw}} - 1$).

(a)	Body mass	Brain mass	Residual brain mass	BMR	Residual BMR	Gestation period	Residual gestation period	Sleep exposure index
SWS time	-0.559	-0.542	-0.038	-0.601	-0.376	-0.552	-0.209	-0.443
<i>P</i> -value	<0.001 (0.002)	<0.001 (0.002)	0.734 (0.025)	<0.001 (0.002)	0.004 (0.004)	<0.001 (0.003)	0.058 (0.006)	<0.001 (0.003)
REM sleep time	-0.363	-0.396	-0.164	-0.377	-0.335	-0.620	-0.520	-0.473
<i>P</i> -value	0.001 (0.004)	<0.001 (0.002)	0.139 (0.008)	0.004 (0.004)	0.012 (0.005)	<0.001 (0.003)	<0.001 (0.003)	<0.001 (0.003)
%REM sleep	0.019	-0.043	-0.195	0.097	-0.084	-0.288	-0.444	-0.190
<i>P</i> -value	0.861 (0.050)	0.698 (0.017)	0.077 (0.006)	0.475 (0.010)	0.541 (0.013)	0.008 (0.005)	<0.001 (0.003)	0.086 (0.007)
(b)	Body mass	Brain mass	Residual brain mass	BMR	Residual BMR	Gestation period	Residual gestation period	Sleep exposure index
SWS time	-0.434	-0.447	-0.130	-0.542	-0.242	-0.438	-0.237	-0.209
<i>P</i> -value	<0.001 (0.002)	<0.001 (0.002)	0.243 (0.010)	<0.001 (0.002)	0.075 (0.006)	<0.001 (0.002)	0.032 (0.003)	0.059 (0.005)
REM sleep time	-0.219	-0.146	0.112	-0.283	-0.336	-0.501	-0.456	-0.314
<i>P</i> -value	0.048 (0.004)	0.190 (0.008)	0.317 (0.017)	0.036 (0.004)	0.012 (0.003)	<0.001 (0.003)	<0.001 (0.003)	0.004 (0.003)
%REM sleep	0.061	0.152	0.219	0.134	-0.139	-0.205	-0.287	-0.202
<i>P</i> -value	0.585 (0.050)	0.172 (0.007)	0.048 (0.004)	0.328 (0.025)	0.310 (0.013)	0.065 (0.005)	0.009 (0.003)	0.069 (0.006)

We note that the correlation coefficients in Table 2a are not statistically valid as the underlying data do not control for phylogenetic non-independence. Alpha was adjusted accordingly following the sequential Bonferroni correction for multiple comparisons (per comparison alphas are in parentheses below each *P*-value such that if the reported *P*-value is less than the parenthetical *P*-value, the relationship remains significant after multiple test correction).

suggest that although some of the correlations identified in previous studies are robust to a phylogenetic control, many are not. We recommend caution in the interpretation of results from earlier studies and suggest that future studies control for shared evolutionary history using phylogenetically based techniques. Future comparative studies of sleep should also venture outside of the dominant mammalian paradigm. For example, in our recent phylogenetic analysis on the correlates of avian sleep, the evolutionary determinants of SWS and REM sleep times were markedly different from those identified in mammals.¹¹⁴ Collectively, such endeavors will only enhance our understanding of why we sleep.

Practice points

- Species cannot be treated as statistically independent units due to phylogenetic relatedness.
- In our phylogenetically controlled analysis (and unlike all previous correlational studies), we found interspecific support for a neurophysiological role for REM sleep, such as memory consolidation, but no comparative support for energy conservation during SWS.
- The incorporation of a phylogenetic control into comparative analyses of sleep yields meaningful differences that affect our understanding of why we sleep.

Research agenda

Evaluating interspecific support for hypotheses for the functions of sleep is essential to our understanding of why animals sleep. The incorporation of phylogenetic controls into such comparative analyses is key to the success of this endeavor. To facilitate this important vein of research, future studies could attempt to:

- Expand the constitutional traits within the existing mammalian data set to more precisely evaluate hypotheses for the functions of sleep.
- Incorporate slow-wave activity as a measure of SWS intensity in addition to time.
- Determine the taxonomic applicability of hypotheses for the functions of sleep by

conducting phylogenetic analyses of sleep in other animal groups.

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