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A phylogenetic analysis of the correlates of sleep in birds

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SUMMARY Quantitative comparative studies of sleep have focused exclusively on mammals. Such studies have repeatedly found strong relationships between the time spent in various sleep states and constitutive variables related to morphology, physiology, and life history. These studies influenced the development of several prominent hypotheses for the functions of sleep, but the applicability of these patterns and hypotheses to non-mammalian taxa is unclear. Here, we present the first quantitative analysis of sleep in a non-mammalian taxon (birds), focusing on the daily amount of time spent in slow-wave sleep (SWS) and rapid-eye movement (REM) sleep as determined by electrophysiological methods. We examined the relationships between constitutive and sleep variables in 23 avian species following earlier studies in mammals, but also considered an index of exposure to predators while asleep and controlled for shared evolutionary history among taxa. Overall, our results were very different from those obtained for mammals. Most remarkably, the relationships between both SWS time and REM sleep time and all constitutive variables were very weak and markedly non-significant, even though we had adequate power to detect correlations typical of the mammalian data. Only an index of exposure to predation during sleep was significantly related to sleep time, which is the only result common to both birds and mammals. Our results suggest that further insight into the function(s) of sleep across the animal kingdom may require an expansion of sleep research beyond the current mammalian paradigm.

KEYWORDS birds, comparative analysis, phylogeny, predation, rapid-eye-movement sleep, slow-wave sleep

INTRODUCTION

The function of sleep is one of the great unknowns in biology (Rechtschaffen, 1998; Siegel, 2005). It is nevertheless clear that all animals studied thus far engage in some form of sleep (Campbell and Tobler, 1984). Sleep has been studied most extensively in terrestrial vertebrates, which show clear differences in neural activity between sleep and wakefulness (Lesku *et al.*, 2006). Sleep in invertebrates is not nearly as well characterized, but recent work shows differences in neuronal firing patterns depending upon behavioral state (e.g. Nitz *et al.*, 2002; Ramón *et al.*, 2004). Furthermore, work at the behavioral (Shaw *et al.* 2000) and genetic (Cirelli *et al.*, 2004, 2005) levels suggest that sleep might be evolutionary homologous across the animal kingdom. In any case, the ubiquity of sleep emphasizes its importance as a biological phenomenon (Shaw *et al.*, 2002).

Even though sleep is a pervasive phenomenon, comparative studies of sleep have focused exclusively on mammals (Allison and Cicchetti, 1976; Elgar *et al.*, 1988; Lesku *et al.*, in press; Meddis, 1983; Siegel, 2005; Tobler, 1995, 2005; Zepelin and Rechtschaffen, 1974). Such studies have repeatedly shown that mammalian sleep is correlated with body mass (Allison and Cicchetti, 1976; Elgar *et al.*, 1988; Meddis, 1983; Siegel, 2004; Zepelin and Rechtschaffen, 1974), brain mass (Allison and Cicchetti, 1976; Elgar *et al.*, 1988; Meddis, 1983; Zepelin and Rechtschaffen, 1974), relative brain mass (Siegel, 2004), absolute and relative basal metabolic rate (Allison and Cicchetti, 1976; Elgar *et al.*, 1988), gestation period (an index of the altricial-precocial gradient, Siegel, 2004, 2005; Zepelin and Rechtschaffen, 1974), and predation risk (Allison and Cicchetti, 1976; Lesku *et al.*, in press; Meddis, 1983). These

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correlates influenced the development of several prominent hypotheses for the functions of sleep (Siegel, 2005), such as the role of slow-wave sleep (SWS) in energy conservation (Berger and Phillips, 1995) and the restoration of important biochemical or physiological processes (Siegel, 2004); the role of rapid-eye-movement (REM) sleep in memory consolidation/learning (Stickgold, 2005), and ontogenetic development of the brain (Roffwarg *et al.*, 1966); and the reduction of REM sleep as an anti-predator adaptation (Allison and Cicchetti, 1976; Lima *et al.*, 2005).

Like mammals, sleep in birds is composed of REM sleep (low-amplitude, mixed-frequency brain activity similar to wakefulness; Tobler and Borbely, 1988) and non-REM sleep (high-amplitude, low-frequency waves, henceforth referred to as SWS). Given the similarity in these two basic components of sleep, one might expect that the correlates of sleep in birds should be similar to those in mammals. To assess this idea, we examined the relationships between sleep (the daily amount of time spent in SWS and REM sleep) and morphological, physiological, and ecological variables in birds in a manner similar to early comparative analyses in mammals (e.g. Zepelin and Rechtschaffen, 1974). Unlike nearly all comparative studies on mammals, however, we control for shared evolutionary history among taxa rather than treating species as statistically independent units (Felsenstein, 1985). Overall, our results indicate that the correlates of avian sleep are very different from those in mammals.

METHODS

Comparative dataset

Our dataset of avian sleep (Table 1) was based upon an intensive literature search including primary literature, book chapters, published meeting abstracts, and our own unpublished data. To be as rigorous as possible, we included only electrophysiological studies that reported daily absolute levels of both SWS and REM sleep for adult birds in non-breeding condition. In an effort to maintain consistency across the dataset, we did not include studies that distinguished unihemispheric SWS from bihemispheric SWS (e.g. Rattenborg *et al.*, 2001). When multiple studies existed for a given species, values were weighted by sample size to produce a species-specific average. One early study was based on pooled data for two species of falconiformes (Rojas-Ramirez and Tauber, 1970) and was therefore excluded from our analysis. All, but three studies (Orange-fronted parakeet, Turkey, and Emperor Penguin) in our dataset maintained animals on an approximate 12 : 12 light : dark cycle. Therefore, the effect of acute changes in photoperiod on sleep (Berger and Phillips, 1994; Rattenborg *et al.*, 2005) was not addressed in our analysis.

Because of technological advances in the field of sleep research during the last 30 years and possible methodological biases across laboratories, we examined the relationship between sleep values and both year of publication and laboratory group using general linear models to test for temporal and laboratory biases in our dataset. Publication date did not have a significant effect on the values of sleep variables (SWS time: $\beta = -0.022$, $T = -0.107$, $P = 0.915$; REM sleep time: $\beta = 0.015$, $T = 0.070$, $P = 0.944$). In addition, the laboratory in which electroencephalogram analysis was performed did not have a significant effect on reported sleep times (SWS time: $F_{6,18} = 1.857$, $P = 0.144$; REM sleep time: $F_{6,18} = 1.688$, $P = 0.181$), suggesting no major methodological biases among laboratories.

Constitutive and ecological variables

Constitutive variables used in this study were the same as those used in previous mammalian comparative studies (Allison and Cicchetti, 1976; Elgar *et al.*, 1988; Lesku *et al.*, in press; Meddis, 1983; Siegel, 2005; Zepelin and Rechtschaffen, 1974): body mass, brain mass, relative brain mass (controlling for body mass), basal metabolic rate, and relative basal metabolic rate (controlling for body mass). We incorporated an ecological variable, exposure to predation risk at the sleep site, based on recent conceptual hypotheses about sleep (Lima *et al.*, 2005) and past comparative work on mammals (Allison and Cicchetti, 1976; Meddis, 1983). We also used incubation period as the only clear analog of the gestation period variable used in previous mammalian studies. We explored the use of developmental state at birth as a direct measure of the degree of precociality. However, developmental state is a highly conserved trait in birds (most variance is at the taxonomic level of order), so when contrasts were applied, too little variance remained to perform a meaningful analysis.

Values for constitutive variables were taken from a given sleep study when available, or from other sources (e.g. Armstrong and Bergeron, 1985; McKechnie and Wolf, 2004; Moller *et al.*, 2005) when unavailable (see Table 1). Relative brain mass, functionally the encephalization quotient (Jerison, 1985), and relative basal metabolic rate were determined for each species using the residuals of a body mass regression with each variable. A few values for brain mass and basal metabolic rate were unavailable in the primary literature and were thus estimated. Brain mass was estimated in four species (white-winged dove, *Zenaida asiatica*; white-crowned sparrow, *Zonotrichia leucophrys*; orange-fronted parakeet, *Aratinga canicularis*; and snowy owl, *Bubo scandiaca*) using endocranial volume according to Iwaniuk and Nelson (2002) from skulls in the collection of the Field Museum (Chicago, IL, USA, see Table 1). Five basal metabolic rate values also required estimation: two were derived from congener values (mourning dove, *Zenaida macroura*, used for white-winged dove, and American crow, *Corvus brachyrhynchos*, used for jackdaw), two from an order-level allometric relationship between body mass and basal metabolic rate (turkey and orange-fronted parakeet), and one from a family-level allometric relationship between body mass and basal metabolic rate (emperor penguin, see Table 1). We emphasize that in no case would even substantial variation in these few estimates affect our qualitative results.

Table 1 Full dataset of sleep, constitutive, and ecological variables for 23 avian species

		Sleep values over 24 h				*Body mass*		*Brain mass*		*BMR*		*Incubation*		*Sleep exposure*	
Species name	*Common name*	*SWS (h)*	*REM (h)*	*n**	*Ref.*†	*Weight (g)*	*Ref.*	*Weight (g)*	*Ref.*	*Rate (W)*	*Ref.*	*Period (days)*	*Ref.*	*Index*	*Ref.*
Anas platyrhynchos	Mallard	7.66	1.41	6, 6	1,2	1252	28	5.8	28	4.07	36	28	40	7.0	40,61,62
Anser anser	Greylag goose	5.77	0.67	7	3	3250	29	11.3	29	10.75	30	30	41	6.5	63
Columba livia	Pigeon	9.74	0.73	8, 3	4,5	265	30	2.4	30	1.72	36	19	42	2.0	42
Streptopelia risoria	Ringneck dove	16.23	0.84	4	6	133	6	1.2	29	0.74	36	14	43	3.0	64
Zenaida asiatica	White-winged dove	8.36	0.80	5	7	154	31	1.4	32	0.74‡	36	16	44	3.0	46
Colinus virginianus	Bobwhite quail	5.47	1.11	–	8	171	29	1.2	29	1.11	36	23	45	5.0	45
Gallus gallus	Chicken	10.56	1.20	17	9	550	29	2.7	29	6.01	36	21	46	4.0	61
Meleagris gallopavo	Turkey	10.40	0.57	10	10	5500	10	7.0	33	12.63§	37	26	47	4.0	61,65,66
Corvus frugilegus	Rook	7.49	0.13	6	11	524	30	7.9	30	3.48	29	17	48	3.0	61
Corvus monedula	Jackdaw	6.51	0.16	8	12	199	30	4.7	30	3.28‡	36	17	48	3.0	61,67
Pica pica	Magpie	7.05	0.05	9	13	215	30	5.3	30	1.20	36	17	48	4.0	61,68
Zonotrichia leucophrys	White-crowned sparrow	6.79	1.32	8	14	28	31	1.1	32	0.34	36	12	49	4.0	49
Fringilla coelebs	Chaffinch	7.48	0.14	5, 4	15,16	24	30	0.8	30	0.37	36	13	50	4.0	69
Taeniopygia guttata	Zebra finch	14.45	0.22	6	2	12	31	0.7	34	0.20	38	13	51	1.0	70
Sturnus vulgaris	European starling	9.19	0.41	3	17,18	109	17	2.2	28	0.88	36	12	52	3.0	71
Turdus merula	European blackbird	7.73	1.37	4, 6	19	93	28	1.9	28	1.15	31	14	53	3.0	53,61
Aratinga canicularis	Orange-fronted parakeet	6.10	0.59	–, 5	20,21	75	21	2.9	32	0.70§	37	30	54	2.0	61
Melopsittacus undulatus	Budgerigar	5.73	0.31	4	22	37	29	1.1	31	0.43	39	18	55	3.0	72
Aptenodytes forsteri	Emperor penguin	9.14	1.36	4	23	28 000	23	46.2	35	45.19¶	37	69	56	7.0	61
Eudyptula minor	Little penguin	6.93	1.34	5	24	960	24	7.4	8	3.73	36	35	57	7.0	61,73
Athene cunicularia	Burrowing owl	13.55	0.73	4	25	120	29	3.0	29	0.87	37	30	58	1.0	58,74
Bubo scandiaca	Snowy owl	7.30	0.36	–	26	2043	31	16.4	32	4.21	36	32	59	6.0	53
Strix aluco	Tawny owl	10.83	0.60	2, –	26,27	475	27	9.4	28	2.08	36	29	60	3.0	75,76

SWS, slow-wave sleep; REM, rapid-eye movement.

*Sample size of studies (separated by commas) used to calculate weighted mean values across studies. In two such cases sample size was unknown (–) for one of the studies, hence the value reported is an unweighted mean.

†References for sleep, constitutive, and ecological values: 1, Ball *et al.*, 1989; 2, Schmidt, 1994; 3, Dewasmes *et al.*, 1985; 4, van Twyver and Allison, 1972; 5, Walker and Berger, 1972; 6, Walker *et al.*, 1983; 7, Ayala-Guerrero and Vasconcelos-Duenas, 1988; 8, N. Ball, D. Schmidt, J. Shaffery, C. Amlaner, unpublished data; 9, Karmanova and Churnosov, 1972; 10, Ayala-Guerrero *et al.*, 2003; 11, Szymczak, 1987a; 12, Szymczak, 1986; 13, Szymczak, 1987b; 14, Rattenborg *et al.*, 2004; 15, Tymicz *et al.*, 1975b; 16, Szymczak and Narebski, 1988; 17, Szymczak, 1987c; 18, Tymicz *et al.*, 1975a; 19, Szymczak *et al.*, 1993; 20, Vasconcelos-Duenas and Guerrero, 1983; 21, Ayala-Guerrero *et al.*, 1988; 22, Ayala-Guerrero, 1989; 23, Buchet *et al.*, 1986; 24, Stahl *et al.*, 1984; 25, Berger and Walker, 1972; 26, Karmanova and Churnosov, 1974; 27, Susic and Kovacevic, 1987; 28, Garamszegi *et al.*, 2002; 29, Armstrong and Bergeron, 1985; 30, Moller *et al.*, 2005; 31, Dunning, 1993; 32, estimates sensu Iwaniuk and Nelson, 2002; 33, Ebinger and Rohrs, 1995; 34, Voigt *et al.*, 2004; 35, Iwaniuk *et al.*, 2004; 36, McKechnie and Wolf, 2004; 37, Vleck and Bucher, 1998; 38, Vezina and Williams, 2005; 39, Rezende *et al.*, 2002; 40, Drilling *et al.*, 2002; 41, Gille *et al.*, 2000; 42, Johnston, 1992; 43, Buntin *et al.*, 1996; 44, Schwertner *et al.*, 2002; 45, Brennan, 1999; 46, Nichelmann, 2004; 47, Eaton, 1992; 48, Marchant *et al.*, 1990; 49, Chilton *et al.*, 1995; 50, Skead, 1960; 51, Fenske and Burley, 1995; 52, Magrath, 1992; 53, Cabe, 1993; 54, Hardy, 1963; 55, Bales, 2004; 56, Bucher *et al.*, 1986; 57, Kemp and Dann, 2001; 58, Haug *et al.*, 1993; 59, Parmelee, 1992; 60, Mikkola, 1983; 61, Skutch, 1989; 62, J. Robb, personal communication; 63, J. Bowler, personal communication; 64, Goodwin, 1977; 65. Chamberlin *et al.*, 2000; 66, R. Kimmel, personal communication; 67, T. Burke, personal communication; 68, Trost, 1999; 69, Lack, 1986; 70, R. Zann, personal communication; 71, D. Wysocki, personal communication; 72, Wenner and Hirth, 1984; 73, T. Rogers, personal communication; 74, R. Poulin, personal communication; 75, A. Vrezec, personal communication; 76, P. Sunde, personal communication.

‡Basal metabolic rates calculated from average of congener; see *Methods* for details.

§Basal metabolic rates calculated from an order-level allometric relationship between body and BMR.

¶Basal metabolic rates calculated from a family-level allometric relationship between body and BMR.

Sleep exposure index was a seven-point scale of risk based upon the exposure to possible predators at the sleep site (Lesku *et al.*, in press). Sleep sites were ranked from 1 (low risk) to 7 (high risk) as follows: 1, sites with limited access to predators, such as burrows or tree holes; 2, sites under logs, in hollow standing trees, or on the sides of cliffs; 3 sites in the tree canopy or a nest in a tree; 4, sites well below the tree canopy at branch junctions; 5, sites on or near the forest floor; 6, sites at ground level with some vegetative cover; and 7, open sleep sites without cover. Reliable descriptions of typical sleep sites could not be found for six species in our dataset. In these circumstances, sleep exposure values were determined according to descriptions of sleep locations obtained through personal communications with authorities on the species in question (see Table 1).

Phylogenetic analysis

To control for shared evolutionary history among taxa, we transformed our comparative data into a set of independent contrasts (Felsenstein, 1985) using Compare 4.6b (Martins, 2004) and a phylogenetic tree of our 23 species derived from Sibley and Ahlquist (1990) (Fig. 1). Branch lengths in this tree could not be reliably determined and thus were set to 1.0 (Garland *et al.*, 1992). Independent contrast analysis examines changes in traits through evolutionary time by calculating the difference in trait values along a series of sister taxa comparisons, yielding statistically independent data. Two-tailed Pearson's product moment correlations were used to compare the relationships between pairs of the resulting (contrast) variables while controlling for multiple comparisons with a simultaneous Bonferroni correction. We also report raw (non-contrast-transformed) correlations for purposes of comparison with earlier mammalian studies. All variables, except REM sleep time, were log transformed before analysis to meet the assumption of normality.

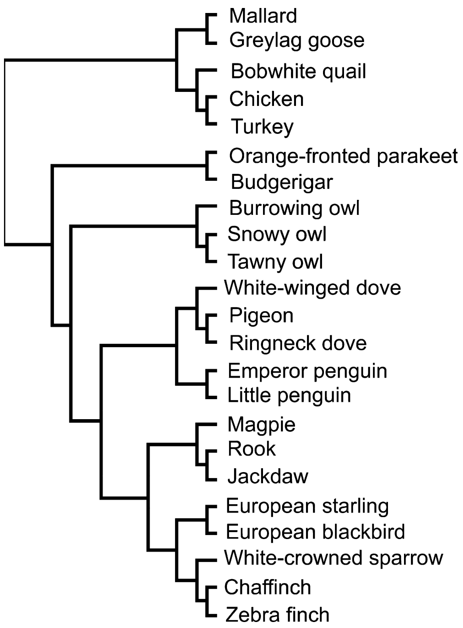

Figure 1. A phylogenetic tree, derived from Sibley and Ahlquist (1990), of the 23 species used in the calculation of independent contrasts. Branch lengths could not be reliably determined and thus were set to 1.0 (Garland *et al.*, 1992).

RESULTS AND DISCUSSION

The well-established mammalian trends documented in previous studies were not apparent in our analysis of avian sleep. Indeed, all relationships between sleep and constitutive variables were non-significant, and effect sizes (correlation coefficients) were generally <0.15 (Table 2a). Specifically, the relationships between residual brain mass (encephalization quotient) and both SWS and REM sleep were markedly non-significant. It would be particularly interesting to examine the relationship between sleep time and specific regions of the brain (e.g. pallial volume), but few such data exist for the species in Table 1. Also non-significant was the relationship between relative basal metabolic rate and SWS. Thus, unlike in mammals, the avian results provide little comparative support for an energy conservation or a memory consolidation/learning role for sleep in birds, although intraspecific support for these ideas exists (e.g. Deregnaucourt *et al.*, 2005; Rashotte *et al.*, 1998). Moreover, we failed to find significant relationships even between SWS and REM sleep and body mass, brain mass, or basal metabolic rate, which are among the strongest relationships observed in mammalian studies (Allison and Cicchetti, 1976; Elgar *et al.*, 1988; Meddis, 1983; Siegel, 2005; Zepelin and Rechtschaffen, 1974). Furthermore, even the strongest relationship in these mammalian studies, that between gestation period and REM sleep, was not significant in our avian study when using incubation period as the analog of gestation period.

We note that these non-significant correlations were also apparent in the raw (non-phylogenetically-controlled) data (Table 2b). Non-phylogenetically-controlled data (also presented in Table 1) are not statistically independent and thus cannot be used to draw firm conclusions about the relationships between sleep and constitutive or ecological variables. However, we included these correlations to point out that even without controlling for phylogeny, strong relationships were not apparent. In fact, none of the raw comparisons were statistically significant (with Bonferroni-adjusted $\alpha = 0.004$) and most of these relationships became even weaker when controlling for phylogeny (compare with Table 2a). As per the main analysis, however, the strongest relationship ($r = -0.518$) was that between SWS and sleep exposure index.

Given the apparent effect sizes in Table 2a, the probability of obtaining biologically meaningful relationships between our sleep variables and the classic constitutive variables is small. In fact, to obtain statistical significance with the effect sizes apparent in Table 2a (assuming power $= 0.80$), we would typically need over a 1000 avian species in our dataset. The small effect sizes in our study contrast with those of

Table 2 Correlations between (a) contrasts for sleep variables and contrasts for constitutive and ecological variables ($n = 22$ contrasts) and (b) raw (non-phylogenetically-controlled) comparisons among sleep, constitutive, and ecological variables ($n = 23$ species)

Sleep variable	*Body mass*	*Brain mass*	*Relative brain mass*	*Basal metabolic rate*	*Relative basal metabolic rate*	*Incubation period*	*Sleep exposure index*
(a) Contrast correlations							
SWS time (*P*-value)	0.004 (0.984)	−0.013 (0.955)	−0.052 (0.817)	−0.019 (0.932)	−0.076 (0.736)	0.042 (0.853)	−0.600 (**0.003**)
REM sleep time (*P*-value)	−0.072 (0.750)	−0.082 (0.717)	−0.042 (0.852)	0.003 (0.991)	0.231 (0.301)	0.133 (0.556)	0.128 (0.570)
(b) Raw correlations							
SWS time (*P*-value)	−0.050 (0.819)	−0.125 (0.569)	−0.246 (0.258)	−0.085 (0.700)	−0.147 (0.514)	−0.094 (0.670)	−0.518 (0.011)
REM sleep time (*P*-value)	0.298 (0.167)	0.116 (0.597)	−0.351 (0.100)	0.286 (0.187)	−0.014 (0.949)	0.345 (0.107)	0.386 (0.069)

Significant *P*-values are in bold font. Bonferroni adjusted $\alpha = 0.004$.
SWS, slow-wave sleep; REM, rapid-eye movement.

mammalian studies, where the correlation coefficients among sleep and constitutive traits were much larger, often in excess of 0.5 or 0.6 (Zepelin *et al*., 2005). Consequently, we had adequate statistical power to detect significant effects in virtually all of our avian comparisons had the observed effect sizes been comparable with those seen in mammals.

The only significant relationship in our phylogenetically-controlled analysis was that between SWS and our predation risk variable, where relatively high levels of exposure at the sleep site were associated with reduced SWS times ($r = -0.600$, $P = 0.003$; Fig. 2). This result not only supports the idea that predation is an important determinant of interspecific patterns in avian sleep, but is also consistent with experimental work on pigeons and ducks (Lima *et al*., 2005; Rattenborg *et al*., 1999, 2001). Another related explanation for our result is that birds that sleep in open environments in the wild may be more sensitive to disturbances in a laboratory setting, thereby reducing the amount of time spent in SWS. In addition, given the strong negative relationships observed between our sleep exposure index and SWS, we might also expect to see a similar relationship with REM sleep. Indeed, mammalian species sleeping in riskier environments engage in less REM sleep (Allison and Cicchetti, 1976; Lesku *et al*., in press; Lima *et al*., 2005; Sanford *et al*., 2003). However, there was no significant relationship between REM sleep time and sleep exposure in our avian dataset (Table 2a), due possibly to the small amount of REM sleep (typically < 10%) observed in birds, which occurs only in brief bouts (Amlaner and Ball, 1994).

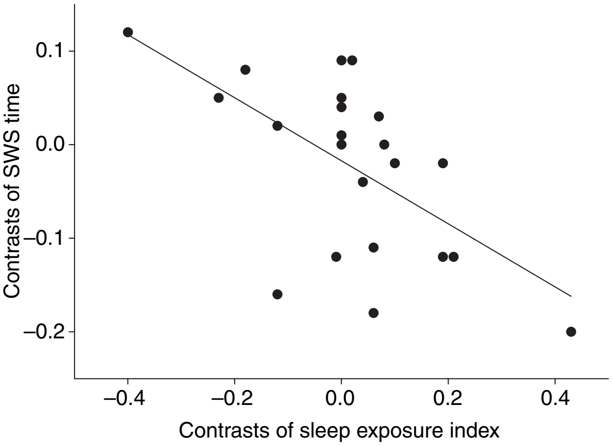

Figure 2. Scatterplot of independent contrasts of time spent in slow-wave sleep (SWS) vs. sleep exposure index. Interpreted directly, the significant correlation ($r = -0.600$, $n = 22$, $P = 0.003$) suggests that an evolutionary increase in sleep exposure is associated with an evolutionary decrease in SWS time. In other words, when phylogeny is controlled, birds that sleep in riskier locations have low SWS times, while birds in safer sleep locations have greater amounts of SWS.

Our results suggest that similarities in the basic components of sleep between mammals and birds may be the result of independent evolutionary processes acting on sleep, and thus may not necessarily reflect similarities in function. It is surprising that we did not find more similarities in correlates of sleep between birds and mammals given the similarities of sleep states at the electrophysiological level. We did find that sleep in both birds and mammals is related to the risk of predation associated with sleep sites, but even here the component of sleep most responsive to such risk differed. We suspect that had birds rather than mammals been the focus of early comparative studies of sleep, the evolution of our views of the function of sleep would likely have been very different (and probably similarly limited in scope) from that realized today. In any case, we hope that our study will stimulate greater interest in the sleep patterns of non-mammalian taxa (Campbell and Tobler, 1984) and prompt further investigation of avian sleep. In particular, future work on birds should focus more on the phenomena of unihemispheric SWS (Rattenborg *et al*., 2000) and the possibility of microsleep (Amlaner and Ball, 1994), both of which are not aspects of sleep in most mammals. Similarly, future work should investigate slow-wave activity in both birds and mammals, as this might be a better measure of SWS than overall time. Collectively, such endeavors are essential to our understanding of not only just sleep in birds, but also sleep in a broader context across the animal kingdom.

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