Journal of Scientific and Technical Research
10 (1 & 2) June & December 2020, 24-29
http://www.publishingindia.com/jstr

Avian Sleep and its Resemblance with Mammals

Anupama Yadav, Raj Kumar, Pragya Verma, Shalie Malik and Sangeeta Rani*
Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, India
*Corresponding Author: sangeetarani7@yahoo.com

Abstract: Sleep, a ubiquitous behavior reported in animal kingdom spreads out from cnidarians to mammals. Evolutionarily it is linked with the development of nervous system which was first time reported in phylum Cnidaria. Thus, this information satisfies a basic function of sleep which is memory processing and information storage. Besides this, cellular restoration and synaptic scaling also encompass as the core function of sleep. Sleep is broadly characterized by the oscillation of NREM (Non-rapid eye movement) and REM (Rapid eye movement) sleep cycles in mammals. Interestingly its distant relative birds also show the same stages while sleeping. Therefore, avian sleep can act as window to understand the mechanisms associated with generation and function of mammalian sleep. Avian sleep shares many similarities with that of mammals, for instance, presence of REM/NREM sleep states which in turn are under circadian and homeostatic control. Likewise minor differences also exist between the two groups for example, the thalamocortical spindles and the ripple complex which are missing from bird sleep. Thus, avian model system can help in understanding the complicacies associated with mammalian sleep (with reference to human) during health and illness.

Keywords: Cellular restoration, Circadian, NREM, REM, Sleep.

I. Evolution of Sleep Across Taxa

How far in the evolutionary history does origin of sleep dates back? Looking at the evolutionary tree sleep can be observed as a conserved behavior prevalent in vertebrates, molluscs, arthropods etc. But on the basis of literature available sleep can be traced back to Cnidarians as they were the first phylum to evolve nervous system [1]. Reports suggest that jellyfish, a member of Cnidaria, undergo periods of extended behavioral shutdown that can be reversed by sensory stimulation [2]. Thus, it can be speculated that sleep co-evolved with neurons. Tracing sleep before Cnidarians is uncertain, as the most phylogenetically ancient animal phylum i.e. Porifera lacks the presence of nervous system and thus, could not exhibit essential features of sleep. Thus, Cnidaria is the oldest extant animal phylum exhibiting sleep like traits in the animal kingdom.

Moving on to vertebrates, the mammalian (human) sleep is basically characterized by the presence of REM and NREM cycles. Besides human, birds have interestingly evolved REM/NREM sleep cycles whereas a hypothetical antecedent to NREM was supposed to exist in reptiles which are a closer relative to avian group than that of mammals. These findings suggest convergent evolution of distinct sleep states in birds and mammals [3]. However, recent EEG recordings reveal the presence of NREM/REM sleep cycles in lizards as well which possess an oscillatory circuit for controlling the balance between the two sleep states [4]. Since, in mammalian brain also NREM and REM were localized in forebrain and brainstem region respectively, thus, the two sleep states might have existed as a coupled mechanism in the amniote lineage of vertebrates [4]. Such an ancient coupling was also supported by the shared developmental origin of REM-, NREM- and wake- promoting neurons in the brainstem [5] along with a positive correlation between REM and NREM sleep duration across evolution [6]. However the phylogenetic origin of the two brain states is apparently not clear. It is assumed that REM state originated before NREM which can be proved by its electrophysiological resemblance with the wake state. REM state evolved as a modification of awake state which has deflected brain's attention inwards away from any sensory stimuli [7] whereas NREM sleep which involves synchronous activity in the neocortex is relatively a late evolutionary adaptation. The presence of NREM sleep in sauropsids also supports this view since the neural circuitry along with the molecules discriminating neocortex from other brain regions in mammals seems to be intact in its analogous regions i.e. dorsal pallium and dorsal ventricular ridge [8, 9, 10]. Sauropsid's also possess thalamus which regulates NREM sleep [11, 12]. The non-amniotic vertebrates lack the presence of REM/NREM sleep traits. This can be proved by studies done in teleost's (for example; zebrafish) which possesses dorsal pallium and dorsal ventricular ridge but lack in thalamocortical loops which controls the frequency and synchrony of NREM sleep waves [13]. But clues to ancestral sleep-regulating systems may be present in these animals, since teleost's thalamus projects as the pallial correspondent of the mammalian hippocampus [13] that generates sharp wave ripples facilitating memory consolidation

during NREM sleep. Remarkably, even in invertebrates, the structural and functional homologs of the two sleep states exist. Thus the evolution of sleep states might represent the neuronal oscillation of the ancestral circuitry that serves to enhance information storage.

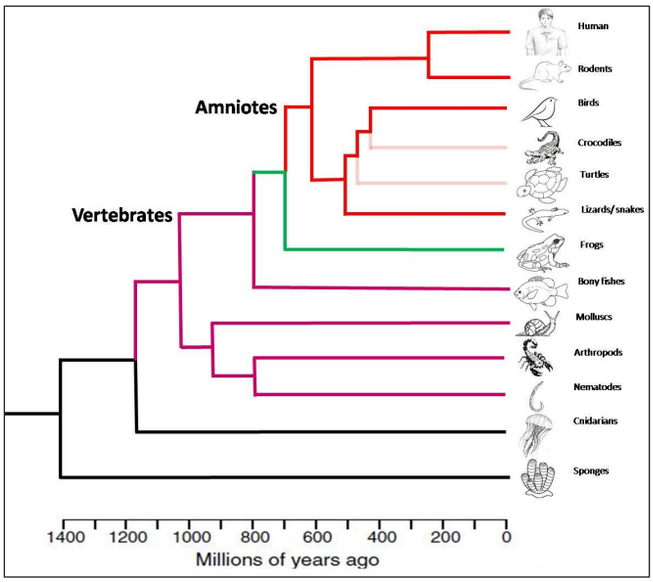

Fig. 1: Cladogram Defining the Evolution of Sleep and its Relationships across Different Phyla

Red line represents groups with REM and NREM sleep. Pink line represents taxa in which these sleep states are expected on the basis of its relatedness with red line group. Green lines represent groups with uncertain sleep outcomes. Magenta lines reflect group with multiple sleep features but not REM/NREM. The figure is redrawn from Joiner *et al.* 2016.

II. Why to Sleep?

Sleep, behaviorally quiescent state which prevents an organism to exploit its environment for feeding, mating and make them more vulnerable to predators. Despite of all these drawbacks sleep is practically unavoidable for organisms. The factors promoting sleep are likely to arise from intrinsic physiological demands which are yet to be recognized. Scientists working from decades have tried to justify sleep via adaptive inactivity and energy allocation hypotheses.

A. Adaptive Inactivity

This idea is driven by the availability of food and safety of an organism. For example, armadillos sleep 20 hours a day whereas its contemporary sloth sleeps for about half of their duration. This behavioral attribute of the armadillos can be explained by the fact, since they are insectivorous in nature and most of the insect availability is during dawn and dusk [14] thus, they spend most of their time sleeping. Secondly, since armadillos inhabit comparatively cool, deep warren that protects them from predators and hot external ambience [15], thus it would energetically wasteful and potentially dangerous to stroll around unnecessarily. The above reason was also used to justify sleep in bats [16]. Besides the above example, daily torpor or seasonal hibernation poses more extreme situations for the animals. In this case, metabolism and arousal threshold are reduced further more than sleep. Thus, sleep can be considered as a midpoint between active and dormant state as it benefits the animal by reduced metabolic rate along with lower arousal thresholds [16, 17]. Taking into account the pervasiveness of sleep/wake cycle an animal requires a balance between the two for its optimum performance.

The hypothesis that sleep might have evolved as a state of adaptive inactivity does not eliminate the other anticipated function of sleep [16] instead it suggests that those functions evolved in species specific manner along with inactivity that lies at core of sleep. But some researchers argued that inactivity was not a function of sleep rather it was a product of the same. This idea was driven from the ontogenetic hypothesis, but focuses on muscle twitching feature of REM sleep. According to this hypothesis, REM sleep evolved as an internal tuning mechanism for sensorimotor circuits during absence of conflicting signals from environment [18]. Recent research indicates that twitching follows a temporal pattern regulated by the brainstem circuits that manifests twitching with increasing frequency with the progression of REM episodes. Since REM sleep precedes wakefulness therefore, some researchers hypothesized that it might have evolved to promote arousal by facilitating feedback from motor neurons [19]. This hypothesis is a more refined version of a previous hypothesis which states that REM sleep evolved to compensate for NREM sleep.

B. Energy Allocation Hypothesis

According to this hypothesis, sleep partitions different biological processes according to the behavioral state to meet the overall energy requirements of the organism [17]. This implies that certain processes are more efficiently performed while awake whereas others during sleep state. Thus the energy allocation hypothesis addresses the loopholes of previous energy related or restorative theories regarding what sleep actually restores. As the whole body metabolism and brain energy reserves (like glycogen and ATP etc.) did not change much across 24 hour cycle, thus, these findings actually support the energy allocation hypothesis. The hypothesis also explains sleep homeostasis resulting from sleep deprivation which arises as a conflict because of shifting of sleep related energy consuming processes during wake hours, which increases sleep drive [17].

The above hypothesis also provides an explanation for the reduced sleep in migratory birds, male pectoral sandpipers and in new born cetaceans. The energy allocation concept is a temporary adaptive feature which directs essential biological processes to wake state which otherwise would occur while

sleeping. Animals which cannot bring about the efficient redirection, suffer negative consequences for the same. For instance, a migratory bird performs worse in an operant task during its non-migratory phase because of lack of seasonal adaptation [20]. Thus, the above hypothesis propounds a core function of sleep in energy conservation.

III. Resemblance between Avian and Mammalian Sleep

A. NREM Sleep

As mentioned earlier in the evolution of sleep, among the amniotes, birds show striking similarity in terms of sleep when compared with the mammals. NREM sleep is characterized by high amplitude slow waves of EEG. Similar to mammals [21], the avian slow wave sleep oscillates between neuronal depolarized and hyperpolarized states [22]. According to a recent study, the slow waves propagate as traveling waves through an avian brain similar to mammalian brain [23] despite of marked cytoarchitectural differences between the two groups [24]. Birds show mammalian like homeostatic regulation of slow wave sleep as it is maximum in the beginning of night and gradually decreases with time spent in NREM sleep [25, 26, 27]. Another similarity between bird and mammalian sleep is in its response towards sleep deprivation. A study conducted on pigeons (*Columba livia*) proved an increment of slow wave sleep in response to 8 hours of sleep deprivation [28]. This study was the first experimental evidence of homeostatic regulation of NREM sleep in birds. Besides pigeon, white-crowned sparrows (Zonotrichia leucophrys gambelli; [29]) showed similar response to sleep deprivation proving it to be a general feature of avian sleep similar to those in mammals. Apart from these two species, the behavioral examination of sleep in a migratory passerine finch, redheaded bunting (Emberiza bruniceps) revealed increased daytime drowsiness and napping because of intense nighttime activity during its migratory phase which again proves mammal like homeostatic regulation of sleep in avian class [30].

B. REM Sleep

Same as NREM, REM sleep also shares certain similarities between avian and mammalian class. REM sleep is represented by low amplitude, high frequency EEG activity similar to that of wakeful state [27, 29, 31]. Besides these EEG representations, REM is also demarcated by reduced muscle tone, rapid eye movement and occasional twitches [31]. In birds, the reduced muscle tone can be visualized behaviorally by gradual drop of head [31, 32] and suspended shivering and panting behaviors [31, 33] similar to mammals.

REM sleep appears to be controlled by both homeostatic and circadian processes of sleep regulation with respect to its timing of appearance and amount in birds. In a diurnal species, time spent in REM sleep gradually increases with the passage of night [25, 26, 27, 28] but discrepancies have been reported in this pattern in some studies [34]. Studies in few species of birds reveal an increased frequency and duration of REM sleep across the night [27, 28]. To confirm the circadian regulation of REM, forced desynchrony experiments are yet to be performed in the avian class [35], but at least these studies indicate towards circadian regulation of timing of REM sleep in both birds and mammals. In addition to the influence of circadian regulation of REM sleep, Tobler and Borbély were the first to show the homeostatic control of REM sleep in 24 hour sleep deprived pigeons [28]. Besides acute deprivation of 24 hour, pigeon subjected to chronic sleep deficit by disk-over-water method [36] or other more effective version [37], demonstrate large increase in REM sleep similar to mammals (sleep deprived rats). Development of REM sleep is also similar in both birds and mammals. In mammals the amount of REM sleep is maximum in early life which reduces as the individual grows in age [7, 38]. This occurs in utero and after birth in altricial species and in utero in precocial species [39, 40]. A recent study in barn owl (*Tyto alba*) nestlings revealed declination of REM sleep with aging [31], although more species need to be investigated with reference to the prevalence and persistence of REM sleep in birds.

IV. Differences between Avian and Mammalian Sleep

The aforementioned text reveals the similarities during sleep in both birds and mammals but as a coin has two faces, similarly, differences do also exist in sleep between the two classes. Several brain rhythms observed in sleeping mammalian brain were missing in birds while asleep [41]. To name, few of them are thalamocortical spindles, the sharp-wave or ripple complexes etc. although birds exhibit slow wave sleep, but mammal-like thalamocortical spindles were missing from the EEG records from a variety of species studied [41, 42]. Besides spindles and ripple complexes of NREM sleep occurring in mammalian hippocampus, grooming, feeding and brief pause of activity have never been reported in avian hippocampus during any sleep state. Consistent with these differences, the theta rhythm of hippocampus in mammals was also missing from different birds studied in past [41]. Therefore, the above information indicates towards a basic difference in processing of hippocampal information between aves and mammals during sleep and wakefulness.

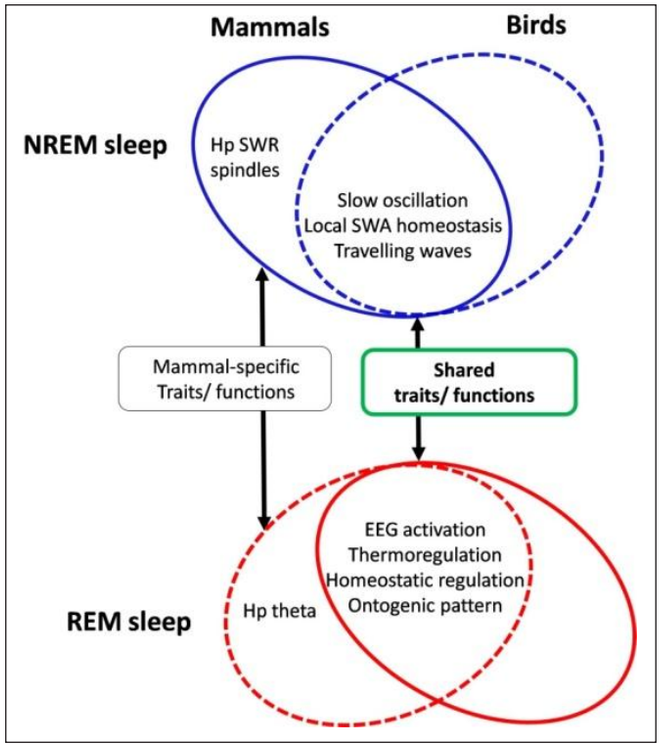

Fig. 2: Similarities and Differences between REM/NREM Traits in Birds and Mammals

The following figure represents the features of REM and NREM sleep which are common between the two classes of vertebrates along with its differences. The figure is redrawn from Rattenborg *et al.,* 2014.

V. Conclusion

The mosaic of convergent and divergent evolution of different sleep traits in mammals and birds provide novel insights into the function and mechanism of sleep in mammals. The greater quantity of REM sleep in early phase of life, its persistence in mature strata of life and rebound after sleep deprivation in both birds and mammals advocate that these are the basic features of REM sleep. Parsimony would suggest that both the avian and mammalian sleep serve the same fundamental function. Talking of NREM sleep suggests that these slow wave oscillations play fundamental role in both the classes. Despite of marked differences in hippocampal memory processing in birds, the confined use-dependent homeostatic regulation of slow wave sleep in both the birds and mammals shares common role of synaptic scaling and cellular restoration occurring locally in the brain. Although birds prove to be an imperfect model for human sleep but they lay in their value for understanding human sleep. Further comparison of sleep between birds and mammals and across the entire animal kingdom might yield auxiliary information in the field of sleep research, which is not readily available following a traditional model based study. Henceforth, a more comparative approach for studying sleep across different animal taxa will likely have greater translational value in better understanding of human sleep during health and illness.

References

[1] H. Watanabe, T. Fujisawa, and T. W. Holstein, "Cnidarians and the evolutionary origin of the nervous system," *Dev. Growth Differ.*, vol. 51, no. 3, pp. 167-183, 2009.

[2] J. E. Seymour, T. J. Carrette, and P. A. Sutherland, "Do box jellyfish sleep at night?," *Med. J. Aust.* , vol. 181, no. 11-12, p. 707, 2004.

[3] R. V. Rial, M. Akaarir, A. Gamundi, C. Nicolau, C. Garau, S. Aparicio, S. Tejada, L. Gene, J. Gonzalez, L. M. De Vera, A. M. L. Coenen, P. Barcelo, and S. Esteban, "Evolution of wakefulness, sleep and hibernation: From reptiles to mammals," *Neurosci. Biobehav. Rev.,* vol. 34, no. 8, pp. 1144-1160, 2010.

[4] M., Shein-Idelson, J. M. Ondracek, H.-P. Liaw, S. Reiter, and G. Laurent, "Slow waves, sharp waves, ripples, and REM in sleeping dragons," *Science*, vol. 352, no. 6285, pp. 590-595, 2016.

[5] Y. Hayashi, M. Kashiwagi, K. Yasuda, R. Ando, M. Kanuka, K. Sakai, and S. Itohara, "Cells of a common developmental origin regulate REM/non-REM sleep and wakefulness in mice," *Science*, vol. 350, no. 6263, pp. 957-961, 2015.

[6] I. Capellini, R. A. Barton, P. McNamara, B. T. Preston, and C. L. Nunn, "Phylogenetic analysis of the ecology and evolution of mammalian sleep," *Evolution*, vol. 62, no. 7, pp. 1764-1776, 2008.

[7] H. P. Roffwarg, J. N. Muzio, and W. C. Dement, "Ontogenetic development of the human sleep-dream cycle," *Science*, vol. 152, no. 3722, pp. 604-619, 1966.

[8] J. Dugas-Ford, J. J. Rowell, and C. W. Ragsdale, "Cell-type homologies and the origins of the neocortex," *Proc. Natl. Acad. Sci. USA*, vol. 109, no. 42, pp. 16974-16979, 2012.

[9] H. J. Karten, "Neocortical evolution: Neuronal circuits arise independently of lamination," *Curr. Biol.*, vol. 23, no. 1, pp. R12-R15, 2013.

[10] H. J. Karten, "Vertebrate brains and evolutionary connectomics: On the origins of the mammalian 'neocortex," *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, vol. 370, no. 1684, 2015.

[11] F. David, J. T. Schmiedt, H. L. Taylor, G. Orban, G. Di Giovanni, V. N. Uebele, J. J. Renger, R. C. Lambert, N. Leresche, and V. Crunelli, "Essential thalamic contribution to slow waves of natural sleep," *J. Neurosci.*, vol. 33, no. 50, pp. 19599-19610, 2013.

[12] M. Lemieux, J. Y. Chen, P. Lonjers, M. Bazhenov, and I. Timofeev, "The impact of cortical deafferentation on the neocortical slow oscillation," *J. Neurosci.*, vol. 34, no. 16, pp. 5689-5703, 2014.

[13] T. Mueller, "What is the thalamus in zebrafish?," *Front. Neurosci.*, vol. 6, p. 64, 2012.

[14] C. M. McDonough, and W. J. Loughry, "Influences on activity patterns in a population of nine-banded armadillos," *J. Mammal.,* vol. 78, no. 3, pp. 932-941, 1997.

[15] A. E. Prudom, and W. R. Klemm, "Electrographic correlates of sleep behavior in a primitive mammal, the armadillo Dasypus novemcinctus," *Physiol. Behav.,* vol. 10, no. 2, pp. 275-282, 1973.

[16] J. M. Siegel, "Sleep viewed as a state of adaptive inactivity," *Nat. Rev. Neurosci.*," vol. 10, no. 10, pp. 747-753, 2009.

[17] M. H. Schmidt, "The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness," *Neurosci. Biobehav. Rev.*, vol. 47, pp. 122-153, 2014.

[18] M. S. Blumberg, A. J. Gall, and W. D. Todd, "The development of sleep-wake rhythms and the search for elemental circuits in the infant brain," *Behav. Neurosci.*, vol. 128, no. 3, pp. 250-263, 2014.

[19] P. L. Brooks, and J. Peever, "A temporally controlled inhibitory drive coordinates twitch movements during REM sleep," *Curr. Biol.*, vol. 26, no. 9, pp. 1177-1182, 2016.

[20] S. G. Jones, E. M. Paletz, W. H. Obermeyer, C. T. Hannan, and R. M. Benca, "Seasonal influences on sleep and executive function in the migratory White-crowned Sparrow (Zonotrichia leucophrys gambelii)," *BMC Neurosci.*, vol. 11, 2010, Art. no. 87.

[21] M. Steriade, "Grouping of brain rhythms in corticothalamic systems," *Neurosci.*, vol. 137, no. 4, pp. 1087-1106, 2006.

[22] A. Reiner, E. A. Stern, and C. J. Wilson, "Physiology and morphology of intratelencephalically projecting corticostriatal-type neurons in pigeons as revealed by intracellular recording and cell filling," *Brain Behav Evol.*, vol. 58, no. 2, pp. 101-114, 2001.

[23] Y. Nir, R. J. Staba, T. Andrillon, V. V. Vyazovskiy, C. Cirelli, I. Fried, and G. Tononi, "Regional slow waves and spindles in human sleep," *Neuron.*, vol. 70, no. 1, pp. 153-169, 2011.

[24] G. J. L. Beckers J. van der Meij, J. A. Lesku, and N. C. Rattenborg, "Plumes of neuronal activity propagate in three dimensions through the nuclear avian brain," *BMC Biol.*, vol. 12, 2014, Art. no. 16.

[25] J. T. Szymczak, W. Kaiser, H. W. Helb, and B. Beszczynska, "A study of sleep in the European blackbird," *Physiol Behav.*, vol. 60, no. 4, pp. 1115-1120, 1996.

[26] N. C. Rattenborg, B. H. Mandt, W. H. Obermeyer, P. J. Winsauer, R. Huber, M. Wikelski, and R. M. Benca, "Migratory sleeplessness in the white-crowned sparrow (Zonotrichia leucophrys gambelii)," *PLoS Biol.*, vol. 2, no. 7, p. E212, 2004.

[27] P. S. Low, S. S. Shank, T. J. Sejnowski, and D. Margoliash, "Mammalian-like features of sleep structure in zebra finches," *Proc Natl Acad Sci. USA*, vol. 105, no. 26, pp. 9081-9086.

[28] D. Martinez-Gonzalez, J. A. Lesku, and N. C. Rattenborg, "Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (Columba livia): Evidence for avian sleep homeostasis," *J Sleep Res.*, vol. 17, no. 2, pp. 140-153, 2008.

[29] S. G. Jones, V. V. Vyazovskiy, C. Cirelli, G. Tononi, and R. M. Benca, "Homeostatic regulation of sleep in the white-crowned sparrow (Zonotrichia leucophrys gambelii)," *BMC Neurosci.*, vol. 9, 2008, Art. no. 47.

[30] A. Yadav, J. Tiwari, V. Vaish, S. Malik, and S. Rani, "Migration gives sleepless nights to the birds: A study on a Palaearctic-Indian migrant, Emberiza bruniceps," *J Ornithol.*, 2020.

[31] M. F. Scriba, A.-L. Ducrest, I. Henry, A. L. Vyssotski, N. C. Rattenborg, and A. Roulin, "Linking melanism to brain development: Expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny," *Front Zool.*, vol. 10, 2013, Art. no. 42.

[32] J. A. Lesku, L. C. R. Meyer, A. Fuller, S. K. Maloney, G. Dell'Omo, A. L. Vyssotski, and N. C. Rattenborg, "Ostriches sleep like platypuses," *PLoS One.*, vol. 6, no. 8, e23203, 2011.

[33] R. Graf, H. C. Heller, S. Sakaguchi, and S. Krishna, "Influence of spinal and hypothalamic warming on metabolism and sleep in pigeons," *Am J Physiol.*, vol. 252, no. 4 Pt 2, pp. R661-R667, 1987.

[34] J. T. Szymczak, "Influence of environmental temperature and photoperiod on temporal structure of sleep in corvids," *Acta Neurobiol Exp (Wars)*, vol. 49, no. 6, pp. 359-366, 1989.

[35] S. B. S. Khalsa, D. A. Conroy, J. F. Duffy, C. A. Czeisler, D.-J. Dijk, "Sleep- and circadian dependent modulation of REM density," *J Sleep Res.,* vol. 11, no. 1, pp. 53-59, 2002.

[36] S. M. Newman, E. M. Paletz, N. C. Rattenborg, W. H. Obermeyer, and R. M. Benca, "Sleep deprivation in the

pigeon using the Disk-Over-Water method," *Physiol Behav.*, vol. 93, no. 1-2, pp. 50-58, 2008.

[37] S. M. Newman, E. M. Paletz, W. H. Obermeyer, and R. M. Benca, "Sleep deprivation in pigeons and rats using motion detection," *Sleep*, vol. 32, no. 10, pp. 1299-1312, 2009.

[38] A. Thurber, S. K. Jha, T. Coleman, and M. G. Frank, "A preliminary study of sleep ontogenesis in the ferret (Mustela putorius furo)," *Behav Brain Res.*, vol. 189, no. 1, pp. 41-51, 2008.

[39] L. Astic, and D. Jouvet-Mounier, "Demonstration of paradoxical sleep in utero in guinea pigs," *C R Acad Sci.*, vol. 269, no. 25, pp. 2578-2581, 1969.

[40] N. Ibuka, "Ontogenesis of circadian sleep-wakefulness rhythms and developmental changes of sleep in the altricial rat and in the precocial guinea pig," *Behav Brain Res.*, vol. 11, no. 3, pp. 185-196, 1984.

[41] N. C. Rattenborg, D. Martinez-Gonzalez, T. C. Roth 2nd, and V. V. Pravosudov, "Hippocampal memory consolidation during sleep: A comparison of mammals and birds," *Biol Rev Camb Philos Soc.*, vol. 86, no. 3, pp. 658-691, 2011.

[42] I. Tobler, and A. A. Borbély, "Sleep and EEG spectra in the pigeon (Columba livia) under baseline conditions and after sleep-deprivation," *J Comp Physiol A.*, vol. 163, pp. 729-738, 1988.