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ORIGINAL PAPER

Evaluation of two minimally invasive techniques for electroencephalogram recording in wild or freely behaving animals

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Abstract Insight into the function of sleep may be gained by studying animals in the ecological context in which sleep evolved. Until recently, technological constraints prevented electroencephalogram (EEG) studies of animals sleeping in the wild. However, the recent development of a small recorder (Neurologger 2) that animals can carry on their head permitted the first recordings of sleep in nature. To facilitate sleep studies in the field and to improve the welfare of experimental animals, herein, we test the feasibility of using minimally invasive surface and subcutaneous electrodes to record the EEG in barn owls. The EEG and behaviour of four adult owls in captivity and of four chicks in a nest box in the field were recorded. We scored a 24-h period for each adult bird for wakefulness, slow-wave sleep (SWS), and rapid-eye movement (REM) sleep using 4 s epochs. Although the quality and stability of the EEG signals recorded via subcutaneous electrodes were higher when compared to surface electrodes, the owls' state was readily identifiable using either electrode type. On average, the four adult owls spent 13.28 h awake, 9.64 h in SWS, and 1.05 h in REM sleep. We demonstrate that minimally invasive methods can be used to measure EEG-defined wakefulness, SWS, and REM sleep in owls and probably other animals.

Keywords EEG recording method · Barn owl · Surface electrodes · Subcutaneous electrodes · Sleep

Abbreviations

EEG	Electroencephalogram
SWS	Slow-wave sleep
TST	Total sleep time
REM	Rapid-eye movement

Introduction

The function of sleep and of the different sleep states still remains unresolved. One approach to gain insight into the purpose of sleep is to examine natural variation in time spent in each state. Comparative work might reveal traits linked to sleep need, but so far all studies (but one) have been done in the laboratory (Lesku et al. 2009). Recordings of animals sleeping in the laboratory may yield misleading results. Depending on the species, there might be

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differences in the degree of habituation to the recording environment that influence the duration and quality of sleep. Moreover, the effect of captivity on sleep may not be in the same direction across species. Certain species may perceive the laboratory to be particularly safe and, therefore, sleep more than in the wild, whereas others may perceive the captive environment to be dangerous and sleep less than in the wild. Such a scenario would be particularly problematic for comparative studies aimed at identifying traits that predict sleep need. Finally, sensory deprivation and resulting 'boredom', ad libitum feeding protocols, social isolation, differences in light and temperature, disturbances by humans, and the absence of predators may alter sleep.

Until recently, studies evaluating sleep times in the field relied on behavioural indicators of sleep such as eye closure. Although behaviour may provide a measure of total time spent sleeping in some species, time spent in specific types of sleep [slow-wave sleep (SWS), and rapid-eye movement sleep (REM sleep)] and sleep intensity cannot be determined without either determining arousal thresholds through disturbing the animal with stimuli of different intensities, or by measuring established electroencephalogram (EEG) correlates of sleep intensity (Tobler 2005). Moreover, in some species behavioural indicators can even completely fail to quantify sleep. For example, observational studies on ostriches (*Struthio camelus*) in the wild rarely describe birds being asleep (Cooper et al. 2010). However, recent electrophysiological recordings have shown that ostriches engage in SWS with their head held upright and eyes open (Lesku et al. 2011). Only during REM sleep does the head drop and eyes close. This led to the wrong impression that ostriches sleep very little, but in fact they actually spend almost half of the 24 h asleep. Such dissociations between behaviour and brain activity-defined sleep occur also in some mammals. Notably, many ruminants exhibit EEG signs of SWS while standing with their eyes partially open and ruminating (e.g., Bell and Itabisashi 1973; Ruckebusch 1972). Collectively, these examples show that behaviour alone may not always provide an accurate measure of sleep.

Historically, despite a long-standing recognition of the need for studies of sleep in the wild (Allison 1972), technical constraints have prevented such studies. Recently, the development of a small and light-weight battery powered recording device (Neurologger 2, Vyssotski et al. 2009) in combination with a minimally invasive EEG recording technique made possible the first study of EEG-defined sleep in an animal recorded in its natural habitat (Rattenborg et al. 2008). Interestingly, the study revealed that sloths (*Bradypus variegatus*) in the rainforest sleep about 6 h less than in the lab (9.63 vs. 15.85 h; Galvão de Moura Filho et al. 1983). Although the reasons for this difference remain unclear, this study demonstrates both the need for further field studies and the feasibility of such studies.

Another technical issue in the study of sleep in nature is the type of electrode placement used for recording the EEG. Although standard epidural electrodes give the most direct recordings of brain activity, they may not be suitable for all species or scientific questions. The method includes an invasive surgery with anesthesia for the placement of epidural electrodes and the animal requires recovery time afterwards. The aim of the present study is to evaluate whether two minimally invasive techniques, surface and subcutaneous electrodes, can be employed for recording the EEG. Both techniques could improve the welfare of animals in experiments and facilitate recordings in the wild.

We chose to study barn owls (*Tyto alba*), because they are large enough to carry a data logger on their head. Also owls are known to exhibit only minor eye movements (Steinbach and Money 1973), a known source of artifacts in recordings with subcutaneous electrodes in birds (Paulson 1964). Barn owls are also a well-established model species for understanding sensory neurophysiology (e.g., Wagner and Frost 1993; Winkowski and Knudsen 2007).

Materials and methods

EEG recordings

Surface electrodes

We recorded the EEG of four adult American barn owls (*Tyto alba pratincola*; three males, one female, age ranging between 8 and 15 years) from the captive breeding stock of the University of Aachen, Germany (50°46′14″N/6°6′19″E). Birds were kept in pairs or individually (one male) and were brought several days before the electrode placement to an inside flight room equipped with perches and an open box. The owls had visual and auditory contact with other owls held in an adjacent aviary. They were also able to hear other owls in the animal housing facility as well as human activity during daytime. Birds were kept on a 13:11 light:dark cycle with lights on at 05:30 and lights off at 18:30. Water was given ad libitum and birds were fed daily 2–3 dead 1-day-old chickens shortly before the onset of the dark phase. As part of previous neurophysiological experiments, each owl had a metal holder implanted on their head (Wagner et al. 2007). Recordings were obtained between December 2009 and April 2010, during the early reproductive period for the owls. Experiments were conducted under a permit from local authorities.

During electrode placement, the owls were held in a laying position with their eyes covered with a cloth to reduce stress. The feathers on top of the head were cut and

five electrodes (Blue Sensor BRS, Ambu, Denmark. modified to an oval size of 7 × 5 mm) were glued symmetrically to the skin with skin glue (Skin Bond, Sauer Continence, Lobbach, Germany). These electrodes were developed for use in recording electrocardiograms in human newborn babies. We used this type of electrodes rather than surface electrodes typically used with humans, because the latter require electrolyte/conducting gel which is prone to drying out. As a result, such electrodes are not suitable for undisturbed multiday recordings in the field. The solid gel surface electrodes were placed over each brain hemisphere, positioned ~6 mm left and right of the sagittal midline over the posterior part of the visual hyperpallium (visual Wulst). Each electrode was referenced to a posterior electrode (~23 mm distance between anterior and posterior electrode) placed over the caudal nidopallium of the same hemisphere and ~7 mm left and right of the sagittal midline. A fifth electrode was centered between the other electrodes and served as a ground (see Fig. 1). The position of the electrodes relative to the mentioned brain areas was verified in a dead owl. Each electrode was held in place with a piece of adhesive bandage (Fixomull stretch, BSN medical, Hamburg, Germany). All electrodes were connected to a data logger (Neurologger 2, 22 × 15 × 5 mm, details are described in Vyssotski et al. 2009; www.vyssotski.ch/neurologger2) and batteries (two Renata zinc-air13, each 1.4 V, 310 mAh; total weight was 5 g). The data logger and batteries were covered with tape and glued with superglue on top of the electrodes. For protection from scratching and removal attempts by the owls, a plastic cover was glued over the electrodes and logger. Bipolar EEG signals from the left and right hemispheres were sampled and recorded at 200 Hz for 5 days for each individual. During this time, the behaviour of the owls was recorded with five infrared-sensitive video cameras per aviary.

Subcutaneous electrodes

To further evaluate the quality of signals obtained from minimally invasive techniques, we also performed recordings using subcutaneous electrodes. Four nestlings of a free-ranging population of barn owls (*Tyto alba*) breeding in nest boxes in western Switzerland were equipped with subcutaneous electrodes. The application of the electrodes was similar to the method used in humans (Ives 2005) and sloths (Rattenborg et al. 2008). In this case, the electrodes were made of fine stainless steel medical wire (diameter 0.13, 2 mm of the insulation exposed; Cooner Wire, Owensmouth, Chatsworth, CA). After anesthetizing the skin on the head (Gingicain, Tetracain 754 mg/65 g), we inserted the electrodes under the superficial layers of skin with a 23-gauge hypodermic needle. Electrodes were held in place and the insertion point was closed with superglue. The electrode positions and other procedures were the same as described above for surface electrodes, with the exception that we did not need to cut as many feathers. In addition, an accelerometer (LIS302DLH; STMicroelectronics) was connected to the Neurologger 2A which recorded acceleration of the head in all three dimensions. With the help of the acceleration recording, it is possible to distinguish between avian wakefulness and REM sleep

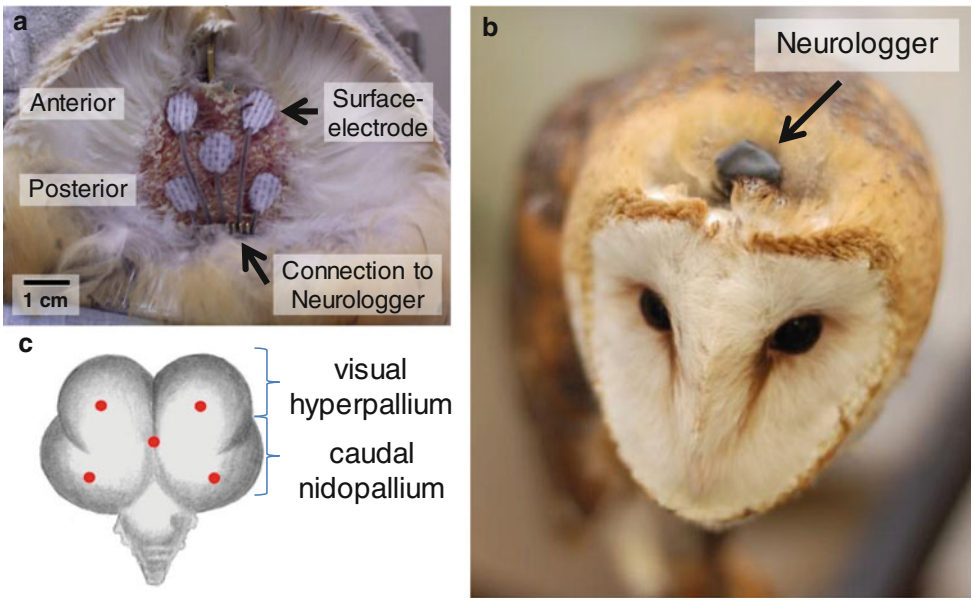

Fig. 1 **a** Head of an adult barn owl with surface electrodes viewed from above. **b** Adult barn owl with surface electrodes and data logger attached to its head. **c** Drawing with the relative placement of the electrodes in relation to owl brain areas

which otherwise requires video recordings to see the dropping of the head or swaying of the whole body typical for REM sleep (Martinez-Gonzalez et al. 2008).

EEG analysis

We present detailed quantitative data for the recordings obtained with surface electrodes and data on the quality of the EEG signals recorded with subcutaneous electrodes for comparative purposes only.

We considered the first 40 h of each recording as a habituation period. The following 24-h period was manually scored for wakefulness, SWS, and REM sleep in 4 s epochs using Somnologica (Medcare, Somnologica Science 3.3.1). Epochs containing more than one state were scored according to the predominant state. Wakefulness was characterized by low amplitude high frequency EEG activity, but was often also accompanied by movement artifacts characterized by high frequency and amplitude activity when the birds were engaged in active behaviour. SWS consisted of low frequency and high-amplitude EEG activity. During SWS, the owls were sitting motionless typically with the eyes completely or nearly closed. EEG activation, a change to low amplitude and fast frequency, arising from SWS was scored as REM sleep when it was accompanied by head dropping (detected via video, see video 1) with closed eyes, and in some cases swaying of the body (as in other bird studies). For the scoring of the EEG of the adults, we used the video recordings to confirm REM sleep epochs. We had acceleration data in parallel with the EEG signals in the recordings of the chicks; therefore, we could use this movement measure for differentiating between wakefulness and REM sleep. Unilateral eye closure, a behaviour associated with inter-hemispheric asymmetries in SWS intensity (Rattenborg et al. 2000) was very rarely observed.

Results

The birds seemed to tolerate the procedure of electrode placement well. They often had their eyes closed and remained still. In the aviary/nest box, the owls seldom showed behaviour such as scratching indicative of an irritation from the electrodes and data logger on their head. After we removed the electrodes, the feathers started to grow back within about 3 weeks in the adults and within about 10 days in the chicks.

Surface electrodes

We obtained EEG signals with the surface electrodes that could be used to readily identify the owls' state (see Fig. 2a). As in other birds, high-amplitude, low-frequency (2–4 Hz) waves distinguished SWS from wakefulness and REM sleep. Power in the >5 Hz band was higher during all states when compared to epidural recordings from other birds including owls. As a result, the signal had to be filtered to facilitate visualization (Fig. 2a).

Also, the quality of the signal degraded with time (decreasing signal-to-noise ratio) making a distinction between states more difficult and impossible in recordings days after electrode placement. The quality of the signals stayed stable and usable for a mean of 89.1 h (range between electrodes 8 and 116 h). The time until the signals were not usable anymore differed between recordings,

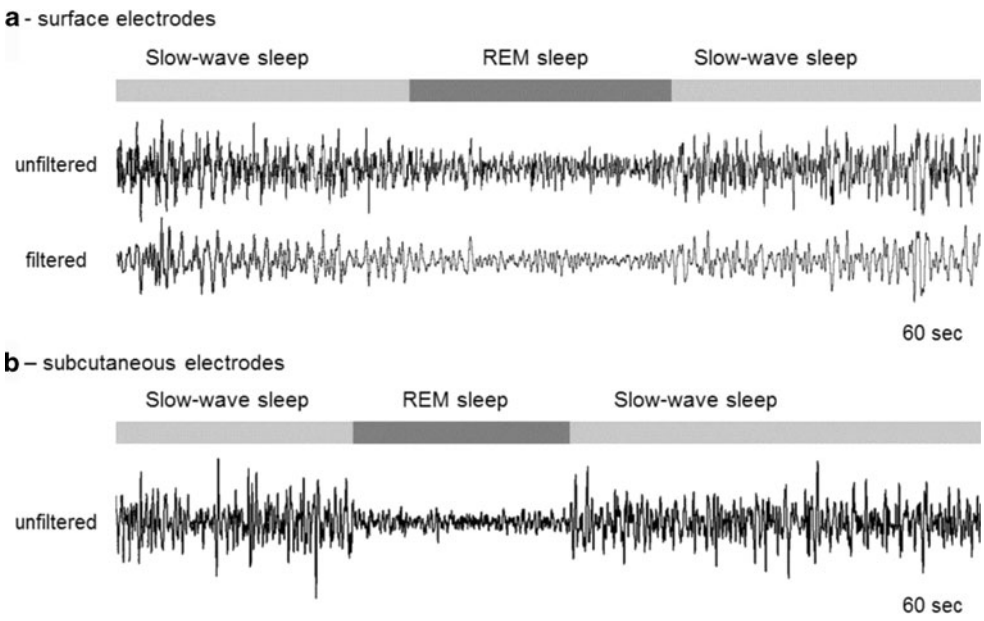

Fig. 2 Signal quality. Example of SWS/REM sleep signals recorded in barn owls with, **a** surface electrodes [*upper channel* unfiltered, *lower channel* bandpass finite impulse response (FIR) filter 1–5 Hz], and **b** subcutaneous electrodes (unfiltered)

probably due to variation in how well the electrodes maintained tight skin contact. Adult owls spent 3.84 h awake (29.5 %), 8.22 h in SWS (63.2 %), and 0.98 h in REM sleep (7.6 %) during the 13 h light phase and were mainly awake during the 11 h dark phase (9.44 h awake 85.8 %, 1.42 h SWS 12.9 %, 0.07 h REM sleep 0.6 %; see also Fig. 3 for total times spent in the three states). The mean duration of SWS and REM sleep bouts was longer during light than during the dark period with two outliers for SWS in the time shortly after lights on and lights off (Fig. 5a), whereas the mean duration of wakefulness bouts was longer during the dark phase than during light. The mean duration of wakefulness bouts ($n = 901$) was 729.22 ± 408.35 s (range 4–3,596 s) and of SWS bouts ($n = 2{,}333$) was 56.40 ± 18.97 s (range 4–1,592 s). REM sleep episodes ($n = 1{,}478$) lasted on average 9.97 ± 1.27 s and the longest REM episode lasted for 60 s (see Fig. 4b for details on the mean time spent in REM sleep over a 24-h period).

Subcutaneous electrodes

The quality of the EEG signal of owl chicks recorded with subcutaneous electrodes was very good during the whole recording period with more distinct changes in amplitude than in the signals recorded with surface electrodes. The signals did not need significant filtering for visualization (Fig. 2b). Amplitude changes between the different states were largely similar to what was described for the tawny owl (*Strix aluco,* Šušić and Kovačević 1973), facilitating the distinction between wakefulness, SWS, and REM sleep. Signal quality was comparable to those recorded with standard epidural electrodes in other bird species.

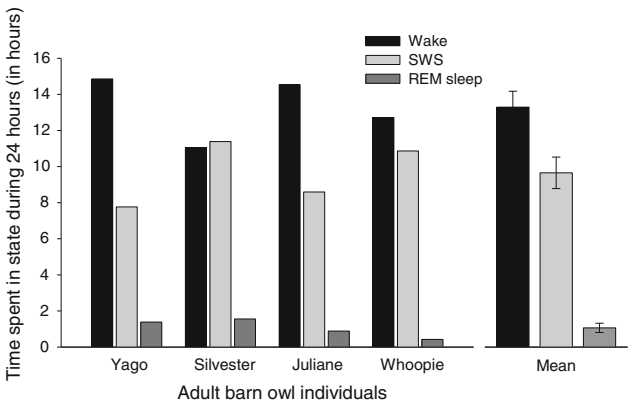

Fig. 3 Time spent in wakefulness (*black bar*), slow-wave sleep (SWS, *light grey bar*) and rapid-eye movement (REM, *dark grey bar*) sleep of four adult barn owls, and the mean (±SEM) times for all owls across a 24-h period

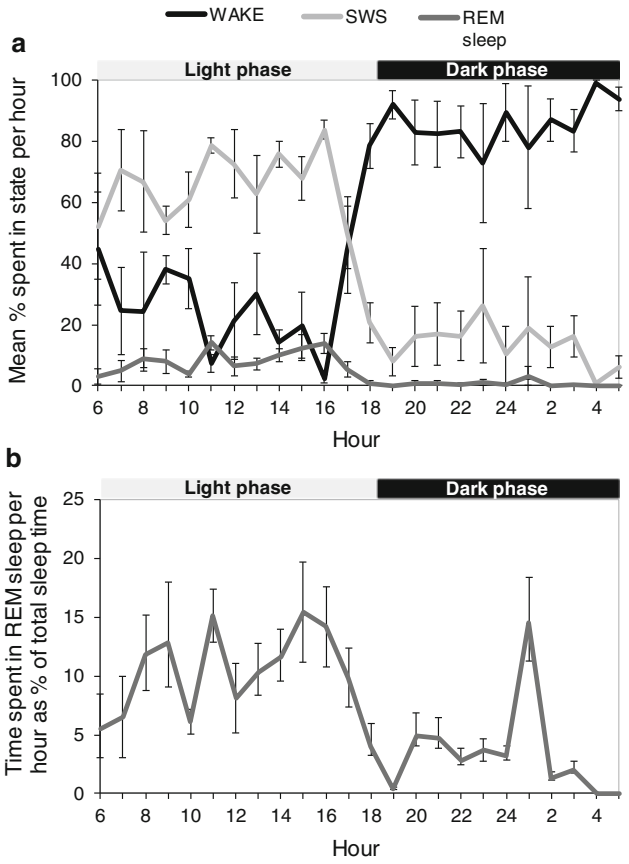

Fig. 4 **a** Percent of each hour (mean ± SEM) spent in wakefulness, slow wave sleep (SWS), and rapid-eye movement (REM) sleep over a 24-h period for four adult barn owls in captivity. **b** Time spent in rapid eye movement (REM) sleep per hour as a % of total sleep time for that hour (mean ± SEM)

Discussion

Sleep in adult barn owls

As expected, all four captive barn owls were nocturnal (Erkert 1969; Taylor 2004; Fig. 4a). Comparisons of the current results with those from previous studies examining sleep in owls (see Table 1) are confounded by differences in recording methods. In all other studies, the owls had intracranial implants attached to a cable. As a result, mobility was limited to a small cage and the birds were not able to fly. In particular, in the study on the snowy owl (*Bubo scandiacus* formerly known as *Nyctea scandiaca)* and one of the studies on the tawny owl (*Strix aluco* formerly known as *Syrnium aluco*), the birds were kept in a whole body restraint during the recordings (Karmanova and Churnosov 1974). Interestingly, the authors describe an unusual fourth state which they called "state of immobility of the cataleptic type" which combined features of wakefulness and SWS that occupied 29.5 and 25.0 % of the birds' behaviour. Given the recording environment and the

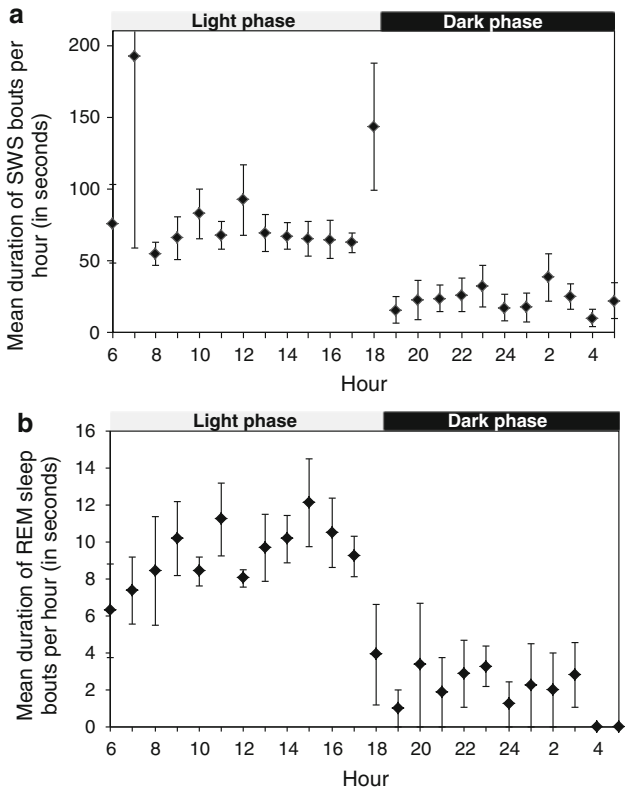

Fig. 5 Duration of SWS (**a**), and REM sleep (**b**) episodes in four adult barn owls over a 24-h period (mean ± SEM)

fact that this state has not been described in other birds and not in the other study on tawny owls (Šušić and Kovačević 1973), this probably does not reflect a normally occurring state. Therefore, the reliability of sleep times from these studies is questionable. In the study on burrowing owls (*Speotyto cunicularia hypugaea*) the birds only rarely closed their eyes during SWS (Berger and Walker 1972), whereas in our study the owls nearly always had their eyes closed during SWS. This might reflect differences in habituation to the laboratory.

The barn owls in our study were housed in aviaries with space to fly and in visual, tactile and acoustic contact to conspecifics. It might be that for this reason, individuals spent more time awake (55.4 %) compared to the other owl species reported in earlier studies, but species differences cannot be ruled out. Also, time spent in REM sleep was the highest among the owl species studied, with 9.9 % (as % of total sleep time). As this state is associated with a higher awakening threshold, it might be the one most likely reduced when individuals are threatened (Lesku et al. 2008). Owls in this study were kept in their familiar environment during the recording and this could have resulted in the higher percentage of time spent in REM sleep.

Comparison of surface and subcutaneous electrodes

We demonstrate that minimally invasive methods can be used to measure EEG-defined wakefulness, SWS, and REM sleep in owls. The application of electrodes and attachment of the data logger is relatively quick and the birds do not need recovery time beyond that related to handling. The duration of recordings with surface electrodes is limited due to degradation of the signal across time. Artifacts arising from the skin/electrode interface and new skin and feather growth likely account for the reduced signal quality. EEG recordings with subcutaneous electrodes had a better signal quality than surface electrodes. The initial differences in signal quality could be due to age (thinner, wetter skull in the chicks) and perhaps due to a greater genesis of slow-waves as seen in adolescent humans (Campbell and Feinberg 2009). Age-related changes in the distribution of maximal slow wave activity

Table 1 Comparison of published data on the percentage spent in wakefulness, slow-wave sleep (SWS) and rapid-eye movement (REM) sleep for different owl species

Species	Wake (%)	SWS (%)	REM sleep (%)	REM/TST (%)	
Snowy owl (*Bubo scandiacus*)	38.2	30.4 (+29.5)[a]	1.9		Karmanova and Churnosov (1974)
Tawny owl (*Strix aluco*)	46.8	25.4 (+25.0)[a]	2.8		Karmanova and Churnosov (1974)
Tawny owl (*Strix aluco*)	33.3	64.5	2.2	3.41	Šušić and Kovačević (1973)
Burrowing owl (*Speotyto cunicularia hypugaea*)	40.5	56.5	3.0	5.31	Berger and Walker (1972)
Barn owl (*Tyto alba pratincola*)	55.4	40.2	4.4	9.91	Present study

Additionally, REM sleep is presented as a percentage of total sleep time (TST). In the study on the sleep of the snowy owl and one of the two on the tawny owl a fourth state (state of immobility of the cataleptic type) is described. Because this state contains features of wakefulness and SWS, no values are given for the percentage in REM sleep as percentage of TST

[a] State of immobility of the cataleptic type

may have also contributed to the difference (Kurth et al. 2010). We followed all equipped chicks during 2–6 weeks after electrode placement and never observed any problems such as infection. The EEG signal proved to be stable over 5 day periods, presumably because these electrodes are less affected by skin or feather growth than surface electrodes. Feathers grew back rapidly, being replaced before the chicks fledged. Both EEG recording methods used in this study are suitable for measuring EEG-defined sleep in animals in the wild.

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