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INFLUENCE OF ENVIRONMENTAL TEMPERATURE AND PHOTOPERIOD ON TEMPORAL STRUCTURE OF SLEEP IN CORVIDS

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Abstract. A survey is presented of the author's own investigations on the effects of ambient temperature and photoperiod on sleep in corvids. Daily sleep patterns of rook, *Corvus frugilegus* and magpie, *Pica pica* have been studied electrographically under natural ambient conditions of light and temperature. The daily amount of total sleep time (TST) was positively correlated with night duration, whereas the proportion of TST spent in paradoxical sleep (PS) was strongly reduced in low ambient temperature (T_a). The mean duration of sleep cycle was found to be positively correlated with T_a. The temporal structure of PS in contrast to that of slow wave sleep (SWS) underwent dramatic changes due to cold exposure. In cold PS episodes appeared randomly throughout the night. The systematic trend observed in nocturnal distributions of SWS did not vary significantly when T_a changed from thermoneutral to moderate cold. This study provided indirect support for the view that PS in birds, like in mammals, is associated with inhibition of thermoregulatory responses.

INTRODUCTION

Many environmental factors are supposedly involved in the temporal patterning of sleep behavior of animals (1,4). The ambient temperature (T_a) is one of these factors which coupled with changes in the thermoregulatory abilities during various states of vigilance may have different consequences for birds. Evidence has been accumulated that changes in ambient temperature affect the structure of sleep in rats, and cause only slight variations in sleep duration (5). However, animals exposed to cold stress exhibit a significant lowering of total sleep time (TST) (7). There are relatively few studies on the effects of thermal stress on sleep in avian species. Stahel et al. (8) have shown a reduction of sleep amount in the little penguin, *Eudyptula minor* during cold exposure. No significant differences have been found in TST of the emperor penguin, *Aptenodytus forsteri* exposed to moderate cold and thermoneutral conditions (3). The effect of thermal stress on sleep pattern has been studied in free-living glaucous-winged gulls, *Larus glaucescens* (6). The daily sleep pattern of captive rooks has been observed under seasonally varied ambient conditions of light and air temperature (12). The temporal characteristic of sleep in the magpie has been compared between two different seasons (13). The large variety of sleep behavior and of its temporal structure among bird species do not allow to generalize unmistakably about the adaptative mechanisms which put constraints on the duration and structure of avian sleep depending on thermal conditions. It is probable that the temporal structure of sleep in birds as well as its duration are, to some degree, a demand of thermoregulatory abilities of a given species.

The aim of the present paper is to survey the effects of ambient temperature and photoperiod on sleep in corvids. The data provide supportive evidence for an active role of thermoregulation in the determination of avian sleep structure.

PHENOMENOLOGY OF SLEEP IN CORVIDS

The electrographic indices of sleep in corvids are essentially the same as those in other avian species. This conclusion has been reached from extended investigations of sleep in the rook, *Corvus frugilegus* (9, 11, 12) and magpie, *Pica pica* (13). A common procedure of EEG recording with a surface monopolar and a depth bipolar electrode was employed to quantitate the states of vigilance. EEG studies were usually joined with simultaneous EOG and EMG recordings. For the purpose of studying the behavioral correlates of sleep and wakefulness some preliminary studies under dim illumination with behavior observations were carried out. However, only the experiments performed under natural lighting and temperature were used to quantify the sleep parameters in corvids. The following vigilance states have been distinguished: wakefulness (W), slow wave sleep (SWS), and paradoxical sleep

(PS). No substantial differences in the electrographic characteristics of a given state were found among the two species. An illustrative example of electrographic recordings is shown in Fig. 1.

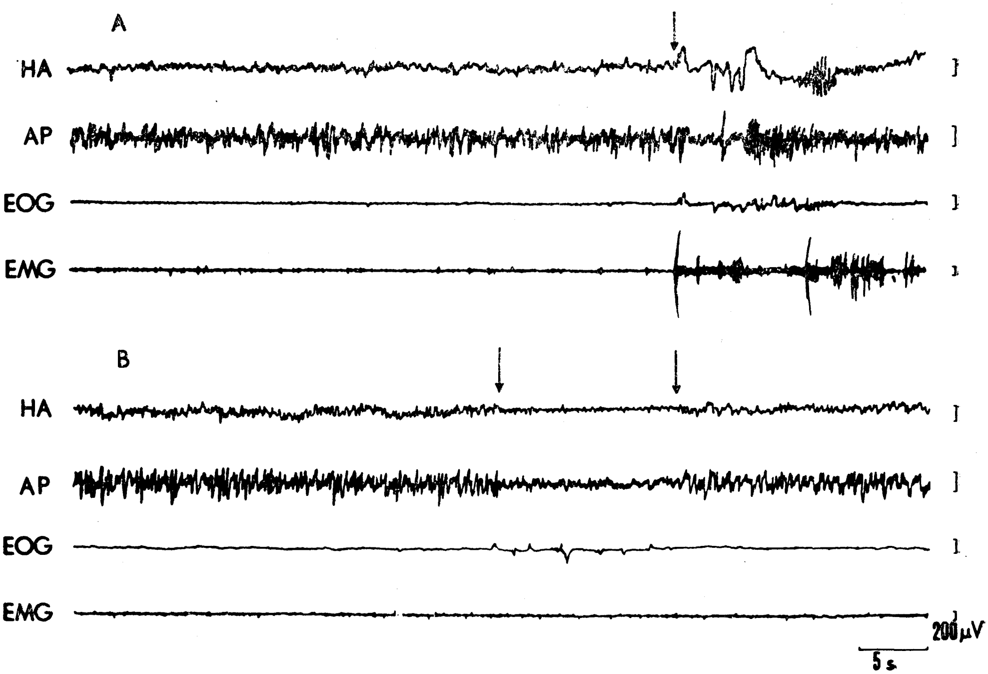

Fig. 1. *A*, slow wave sleep terminated by wakefulness. *B*, slow wave sleep interrupted by an episode of paradoxical sleep. HA, hyperstriatum accessorium; AP, area paraentorhinalis; EOG, electrooculogram; EMG, electromyogram.

During wakefulness the corvids exhibited various behavioral categories from active behavior to a resting posture with eyes open, EEG was characterized by a low voltage (40-50μV), high frequency (8-10 Hz) activity. EMG of awake birds showed a high tonic activity with frequent components associated with body and head movements. A close connection of the level of EMG activity with exogenous stimuli was seen. The EOG records exhibited frequent complex conjugate eye movements. When birds were motionless with eyes open the EEG records became sometimes polymorphic, i.e. a short period of high voltage ($>200\ \mu V$) and low frequency (<4 Hz) activity appeared. These so-called drowsiness bouts were not recognized as a separate state.

Drowsiness usually preceded the onset of sleep. The sleeping posture was characterized by the head drawn into the breast and the bill pointed forward. It occurred in more than 40% of total sleep time. SWS was reflected by a synchronized high voltage EEG (80-250 μV) with a strong low frequency component (3-4 Hz). Neck EMG was essentially lower than that of wakefulness but without phasic components. During sleep the eyelids were closed or sometimes open. Occasional increases in EOG activity resulted from slight nictitating membrane movements.

Episodes of PS always followed SWS and the onset of PS was behaviorally indicated by head dropping. EEG showed a wakefulness-like pattern. The EMG amplitude was not lower comparing with that observed in SWS. Nevertheless, in some cases hypotonia was observed during PS. The eyes were usually completely closed. Most PS episodes were associated with clusters of eye movements. Neither hippocampal theta EEG activity nor spindles were observed in either of the two species of corvids investigated.

SLEEP IN THERMONEUTRALITY AND COLD

Sleep pattern

All results reported were obtained using wild rooks and magpies trapped locally (53°02′N, 18°35′E) and well habituated to laboratory conditions. The birds were subjected to natural lighting and temperature.

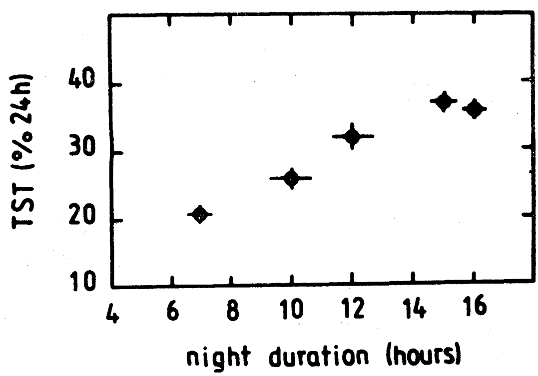

Fig. 2 Relation between total sleep time (TST) and night duration in rooks. Values shown are means with SEM from experiments carried out on 5-9 birds.

The daily percentage of total sleep time in the rooks increased gradually with the duration of the night (Fig. 2). In natural summer light-dark

(LD) 17 : 7 conditions TST constituted 21.1% of the 24-h, whereas in winter (LD 8 : 16) the daily value of TST reached 35.4%. Since LD varied simultaneously with T_a it was impossible to determine the effect of ambient temperature on TST.

The proportion of TST spent in PS was strongly affected by ambient temperature in both species of corvids (Fig. 3). During cold (T_a −4 to +5°C) the amount of PS was below one percent. When ambient temperature increased from 5 to 15°C the percentage of PS rose nearly three

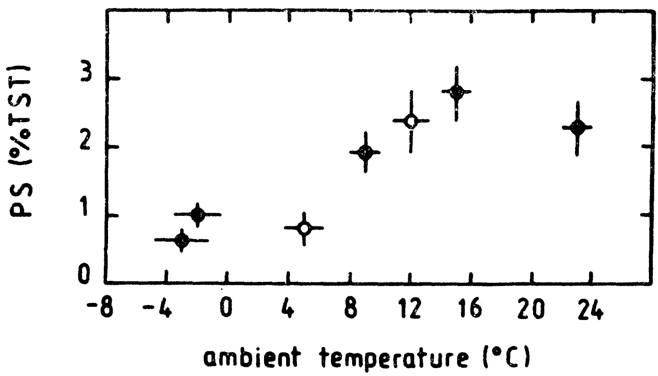

Fig. 3 Relation of the percentage of paradoxical sleep (PS) to ambient temperature in rook (filled circles) and magpie (open circles). Six magpies under LD 14:10 conditions were used. Other explanations as in Fig. 2.

times. On the other hand, in the rooks exposed to $T_a = 23°C$ a slight lowering in PS was observed. The effect of ambient temperature on PS percentage was established but quantities in Fig. 3 for rooks should be treated with care because influences of varied LD and season could not be excluded.

Sleep cycle (SWS + PS) duration underwent significant variations in response to ambient temperature (Fig. 4). A clear increase of the mean duration of sleep cycle was observed in the rooks with increasing T_a. A point ($T_a = 15°C$) slightly skewed from this trend was obtained in April. This period in the free-living rooks is known as breading season. In the magpies under the same LD conditions the duration of sleep cycle was shorter in lower ambient temperature. Moreover, Fig. 4 shows that duration of sleep episodes in the magpies was markedly shorter than in the rook. This fact could be interpreted in terms of interspecies differences in the brain weight and metabolic rate (2).

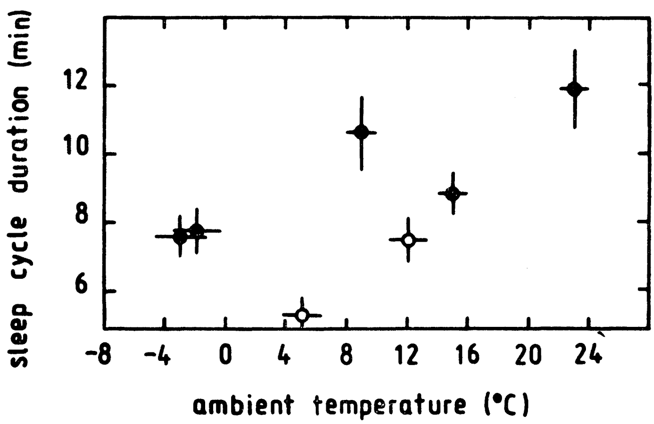

Fig. 4 Relation of the sleep cycle duration to ambient temperature. See legends of Fig. 3 for details.

Temporal structure of sleep

The both corvids studied are typical diurnal birds which spend day time in active wakefulness. The episodes of wakefulness and both sleep states exhibited a sequential nature. However, the temporal structure of sleep and wakefulness observed in the rook varied as a function of ambient temperature. Cold exposure induced longer episodes of W, while PS episodes were significantly shortened as compared with those under thermoneutral conditions. Analysis of the time course of SWS bouts showed that the hourly percentage of SWS increased throughout the night. A similar trend was observed in the distribution of mean duration of SWS periods. These patterns failed to differ significantly when ambient temperature changed from −4 to 23°C. However, the temporal structure of paradoxical sleep underwent dramatic changes due to cold exposure. Figure 5 shows the distribution of hourly percentage of PS obtained at near thermoneutral and cold temperatures. During cold exposure PS occurred rather evenly throughout the night. A lowering of the PS value resulted mainly from reduction of the number of episodes. In thermoneutral conditions a clear decreasing trend in PS was seen.

Polygraphic studies of sleep in the starling at thermoneutrality have shown that the daily distributions of PS were constant under various LD conditions (10). Thus cold temperature severely disordered the daily PS patterns, and their temporal structures could be considered as responses to the thermal conditions. On the other hand, the PS to TST ratio in the emperor penguin was constant under natural antarctic summer temperature (−8 to −17°C) (3). Unfortunately, the temporal structure of PS in the above species has not been analysed. In the corvids studied the ambient temperature had no effect on the probability of transition of PS into W. The lowest probability of 0.07-0.08 was observed at $-2°C$ and 23°C T_a in winter and summer, respectively. A significant increase in the number of PS episodes terminated by W occurred

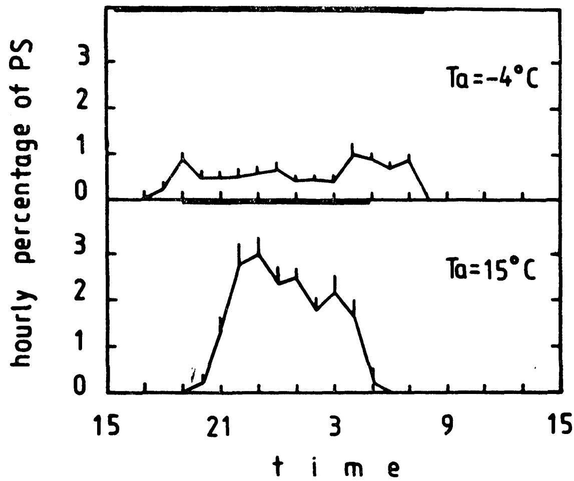

Fig. 5 Daily course of paradoxical sleep (PS) hourly percentage in two ambient temperatures (T_a). The night in each T_a indicated by black bar below top abscissa.

in late autumn and early spring. Therefore we suppose that in the studied corvids under cold, paradoxical sleep poikilothermy does not facilitate arousal as it has been postulated in mammals (14).

CONCLUDING REMARKS

The paper deals with the effect of thermal cold stress on the temporal sleep structure in two species of corvids. These avian species when free-living in Central Europe are often exposed to severe environmental conditions with air temperatures from -25 to 30°C. Experiments with naturally varied LD and T_a failed to show conclusively the effect of thermal loading on total sleep time. They suggested that natural lighting was the primary factor which regulated TST. The mean duration of sleep cycle was strongly affected by thermal conditions. Since SWS constituted the majority of the sleep cycle, we concluded that cold temperature slightly reduced the percentage of SWS. On the other hand, the temporal structure of SWS episodes was marginally influenced by ambient temperatures ranging from $-4°$ to 23°C. The cold hardly affected the amount and temporal structure of PS. A significant lowering of time spent in PS could be interpreted as a cold defensive mechanism. We suppose that in the studied birds during PS the thermoregulatory abilities were decreased, and inhibition of PS was the response to achieve heat balance of the organism.

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