

Sleep and metabolic rate in the little penguin, *Eudyptula minor*

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Summary. The effects of sleep upon metabolic rate in the little penguin were examined at thermoneutral and low temperatures in day and night experiments.

Little penguins show similar electrophysiological indices of sleep to other birds. The amount of sleep increased at night due to increased frequency of sleep periods and decreased with cold exposure due to a reduction in the length of sleep periods.

Sleep was associated with a slight decrease (8%) in metabolic rate when compared to quiet wakefulness in all experimental conditions. This decrease, however, represents only a marginal reduction in daily energy costs. There would be a difference of only 2.4% in the hypothetical daily energy budget of a resting little penguin if it did not sleep at all.

Introduction

Thermoregulatory mechanisms vary as a function of sleep and wakefulness in mammals. Slow wave sleep (SWS) is accompanied by a regulated decrease in the set-point for body temperature regulation and paradoxical sleep (PS) is further associated with a profound inhibition of thermoregulatory responses (Heller and Glotzbach 1977; Parmeggiani 1980). In association with these changes in thermoregulatory functions, ambient temperature influences sleep. Total sleep time (TST) is maximal at thermoneutrality and the amount of sleep, particularly PS, decreases in hot or cold con-

ditions (Parmeggiani and Rabini 1970; Sakaguchi et al. 1979).

Information on sleep in birds is relatively sparse compared to that in mammals. The electrophysiological indices of sleep in birds are broadly similar to those in mammals although PS epochs in birds are very brief (approximately 10 s) (Goodman 1974; Ookawa 1972). Physiological changes during sleep in birds also appear to be similar to the mammalian pattern. Pigeons show a decrease in body temperature set-point during SWS and a cessation of shivering and panting was observed during PS (Graf et al. 1980). Hohtola et al. (1980) demonstrated that shivering diminished during sleep at low temperatures in the pigeon although not all thermoregulatory responses were attenuated since ptiloerection during sleep was enhanced with respect to wakefulness.

The decrease in thermoregulatory effector mechanisms during sleep has been regarded as support for the view that sleep is an energy conserving process (Walker and Berger 1980). Direct evidence for this proposal is scarce. There have been relatively few studies which have investigated sleep and metabolism in animals without manipulation of hypothalamic or spinal cord temperature so that the importance of the observed thermoregulatory changes is unclear. Available evidence suggests that sleep is associated with a slight decrease in metabolic rate of approximately 10% in comparison to quiet wakefulness (Toutain et al. 1977; Passmore and Durnin 1955).

This study investigates the effect of sleep on metabolic energy expenditure in the little penguin at thermoneutrality and low ambient temperature. In addition, since body temperature regulation in birds follows a diurnal rhythm which is actively adjusted between day and night (Graf 1980a, b),

Abbreviations: EEG electroencephalogram; EMG electromyogram; PS paradoxical sleep; SWS slow wave sleep; TST total sleep time

the influence of sleep upon this cycle was examined.

Materials and methods

The five penguins used in this study were maintained under the same conditions as reported previously (Stahel and Nicol 1982). Mean body weight during experiments was 0.96 ± 0.11 kg. Penguins were released at the capture site on completion of experiments.

Electrodes were implanted under halothane anaesthesia for chronic recordings of electrophysiological indices of sleep and wakefulness. EEG (electroencephalogram) electrodes were made from stainless steel or goldplated brass wood screws. These were implanted in the skull above the dura of the Wulst to record bipolar electrical activity of the brain. Electro-oculogram electrodes monitored eye movements. These electrodes consisted of fine copper or stainless steel wires inserted under the inner and outer canthus of one eye or under the outer canthus of both eyes. EMG (electromyogram) electrodes were used in two penguins to record dorsal neck muscle activity. The electrodes were made from fine multistrand insulated stainless steel wires joined at the end by a ball of dental cement. A small area of teflon insulation was removed from each wire near the junction. Lead wires from recording sites were soldered to a multipin socket which was mounted on the skull with dental acrylic cement. Electrodes remained in place for two months and were removed from each bird when they became loose, presumably due to bone absorption around the screws. At least one week was allowed following surgery before experiments commenced.

Electrophysiological parameters were recorded on a Grass model 79D polygraph via a braided cable and slip ring connector. Chart speed was 5 mm/s. Polygraph records were scored in 5 s periods for sleep/wakefulness analysis and each minute for comparison with metabolic records. Data from two penguins were also recorded on magnetic tape for subsequent analysis of EEG characteristics.

Oxygen consumption and carbon dioxide production were measured with a fast response open circuit system to avoid mixing air samples from different states of consciousness. The metabolic chamber consisted of a seven litre coffee tin immersed in brine, the temperature of which was controlled by circulation through a heater/cooler unit. Room air was drawn through the chamber with a Thomas compressor and the airflow rate (7.93 ± 1.45 l/min) measured with a calibrated Gilmont flowmeter. The outlet air was dried with silica gel and passed to the sample channel of a Servomex OA 184 oxygen analyzer. Atmospheric air simultaneously passed through a flowmeter and silica gel to the reference channel of the analyzer. Dry outlet air was also drawn through a Beckman LB-2 Medical Gas Analyzer for measuring carbon dioxide production. Outputs from the gas analyzers were separately recorded on a Rikadenki recorder with 1% full scale deflections.

The expected time lag for a stepwise change in V_{O_2} or V_{CO_2} was calculated from the equation of Christenson (1947, quoted by Westerterp 1977):

$$Q/P = 1 - e^{(-Ft/V)}$$

where Q/P = the ratio of change in amount of O_2 or CO_2 carried off to the change in oxygen consumption or carbon dioxide production (l/min); F = air flow (l/min); V = net volume (l); and t = time after start of change (min).

The volume of the chamber and airlines in the system was 9.23 l and the volume of a one kg penguin was calculated by displacement to be approximately 1.3 l. Hence a 95% response

could be expected in three minutes and a 98% response in four minutes after a stepwise change in expired gases in the system. From these estimated equilibration times the first three minutes of metabolic record after a change of state of consciousness were ignored to account for lag time in the system.

Metabolic records were scored for sleep or wakefulness from polygraphic recordings and the mean concentration of expired gases in sample periods determined by tracing the record onto standard weight paper which was weighed to the nearest 0.1 mg. Metabolic records were considered acceptable for analysis if (excluding lag time) they showed five minutes or more of continuous sleep or quiet wakefulness. Due to the very short period of PS episodes, it was not possible to distinguish PS from SWS in metabolic analysis and hence sleep was considered as a single state.

Sleep-waking patterns and metabolic rates were measured at thermoneutrality (21.3 ± 2.7 °C) and in cold conditions (-1.8 ± 2.2 °C). No experiments were attempted above the upper critical temperature since little penguins cannot withstand prolonged exposure to heat stress (Stahel and Nicol 1982). During day experiments an equilibration time of at least one hour at thermoneutrality and two hours in the cold was allowed before data were collected. Penguins were fed in the afternoon before an experiment commenced the following day. Measurements from day experiments were taken from 12:00 to 16:00 h. For night experiments penguins were introduced to the chamber at 17:00 h and data collected for a four hour period at least two hours after dusk. Illumination in night experiments was provided by a dim red light above the recording instruments.

Sleep characteristics and sleep patterns from each experimental condition were compared by two-way analyses of variance with unequal but proportional subclasses. Metabolic data for sleep and wakefulness in each experiment was averaged and compared with paired t -tests.

Results

Polygraphic indices of sleep and wakefulness in the little penguin are shown in Fig. 1. Wakefulness was characterized by frequent eye movements and low voltage, relatively high frequency EEG activity (50 μ V, 13–17 Hz) interspersed with bursts of slow waves (130–180 μ V, 8–12 Hz). Slow waves were more prominent during quiet wakefulness.

Penguins in their enclosure were observed to sleep either standing or lying down with the head retracted into the body and the beak pointing slightly upwards in each case. Due to the small size of the metabolic chamber, the penguins slept upright during experiments. Polygraphic records of SWS (Fig. 1B) showed no eye movements apart from small voltage fluctuations probably associated with contraction of the nictitating membrane. The EEG was characterized by synchronous activity of high voltage, relatively slow waves (100–200 μ V, 8–12 Hz). Paradoxical sleep episodes of short duration were interspersed throughout SWS. These epochs were identified by clustered eye movements and desynchronized EEG patterns which resembled those seen during active wakefulness (< 50 μ V, 13–14 Hz).

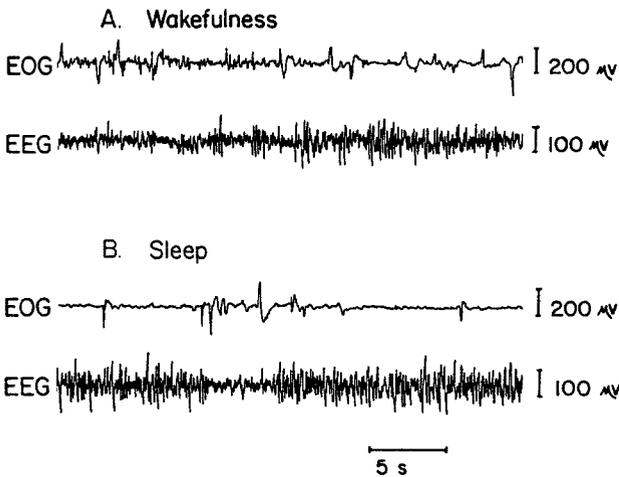


Fig. 1A, B. Polygraphic indices of sleep and wakefulness in the little penguin. A Wakefulness. B Slow wave sleep interrupted by an episode of paradoxical sleep. EOG electro-oculogram measuring eye muscle activity; EEG electroencephalogram measuring surface electrical activity of the forebrain

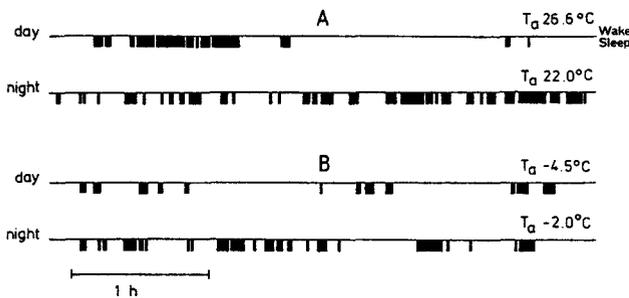


Fig. 2A, B. Sleep-waking patterns of a little penguin during four hour polygraph recordings. Each minute was scored as either wakefulness or sleep (slow wave sleep plus paradoxical sleep). A Thermoneutrality. B Cold exposure. Areas shaded black represent periods of sleep

Neck muscle activity correlated poorly with sleep and wakefulness. Although EMG bursts were associated with activity during wakefulness, the EMG was isotonic during quiet wakefulness and SWS. PS episodes occasionally showed a decrease in muscle tone but more often EMG bursts due to jerks of the head were observed.

Sleep-waking patterns

The amount of sleep observed in the little penguin varied as a function of its circadian rhythm and ambient temperature. Figure 2 shows the temporal sequence and amount of sleep in the same penguin in each experimental condition.

There was no significant difference between the duration of SWS and PS episodes with day and

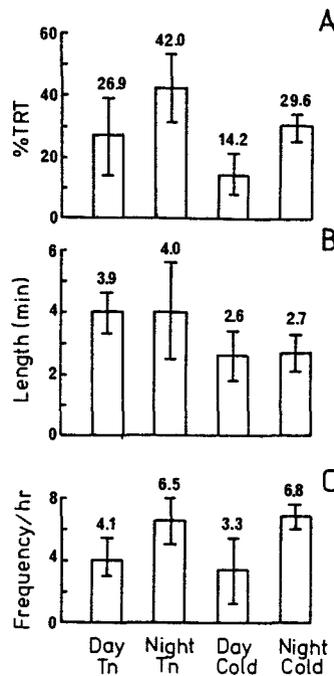


Fig. 3A-C. Mean characteristics of sleep in the little penguin from four-hour recordings at thermoneutral and cold temperatures in day and night experiments. A Amount of sleep. B Duration of sleep periods. C Frequency of sleep periods. Standard deviations are shown by vertical lines. Each bar represents 8 experiments at thermoneutrality and 4 experiments in cold temperatures

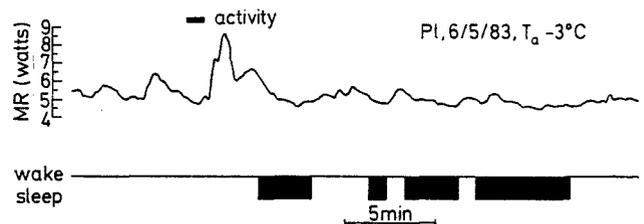


Fig. 4. Record of metabolic rate during sleep and wakefulness in a little penguin at night in cold conditions. Areas shaded black represent periods of sleep. Note effects of activity upon metabolic rate

night recordings at different temperatures. The mean length (\pm SD) of SWS episodes from all conditions was 41.7 ± 8.60 s ($n=24$) and the mean length of PS episodes was 8.3 ± 0.96 s. The relative proportions of SWS and PS within sleep also did not significantly differ with day and night and temperature. Mean percentage of PS to total sleep time from all conditions was 16.2 ± 4.74 .

Figure 3 shows the amount of sleep, the duration and frequency of sleep periods of little penguins derived from four hour polygraphic recordings during day and night experiments in thermoneutral and cold temperatures. Total sleep time

Table 1. Metabolic rate (Watts) of little penguins during sleep and quiet wakefulness at thermoneutral and cold temperatures in day and night experiments

	Sleep ^a	Wakefulness ^a	Δ MR ^b	% Wakefulness ^c	Probability
Day, thermoneutrality	3.87 ± 0.54	4.18 ± 0.44	-0.31	92.6	(<i>t</i> = 3.10, <i>n</i> = 8, <i>P</i> < 0.02)
Night, thermoneutrality	3.50 ± 0.48	3.74 ± 0.59	-0.24	93.6	(<i>t</i> = 2.66, <i>n</i> = 6, <i>P</i> < 0.05)
Day, cold	5.49 ± 0.90	5.89 ± 0.77	-0.40	93.2	(<i>t</i> = 4.52, <i>n</i> = 6, <i>P</i> < 0.01)
Night, cold	5.00 ± 0.76	5.54 ± 0.66	-0.54	90.3	(<i>t</i> = 5.75, <i>n</i> = 4, <i>P</i> < 0.02)

^a Mean ± standard deviation

^b Δ MR = sleep - wake

^c % Wakefulness = sleep/wakefulness × 100

in penguins increased at night compared to day experiments ($P < 0.005$) (Fig. 3A). This increment of 15.1% at thermoneutrality and 15.4% in cold conditions was due to an increase in number rather than the length of sleep periods ($P < 0.001$) (Fig. 3C). Exposure to cold reduced total sleep time during both day and night experiments ($P < 0.025$) (Fig. 3A). The reduction of 12.7% in day experiments and 12.4% at night was the result of a reduction in the length of sleep periods ($P < 0.025$) (Fig. 3B).

Metabolic rate

Figure 4 shows a representative sample of metabolic rate with sleep and wakefulness in one penguin. Metabolism varied with the amount of muscular activity but remained relatively constant during quiet wakefulness and sleep. Arousal was often associated with an increase in metabolic rate, probably due to muscular activity. The mean levels of metabolism during sleep and quiet wakefulness in each experimental condition are given in Table 1. Metabolic rates in this study were slightly lower than previously reported (Stahel and Nicol 1982) due to short sample periods and high air flow rates.

Metabolic rate varied between day and night experiments. During wakefulness at thermoneutrality metabolism was 0.44 Watts lower at night than in day experiments. A similar difference of 0.35 Watts was seen during wakefulness in day and night experiments during cold exposure.

In all experimental conditions, metabolic rate significantly decreased during sleep in comparison to quiet wakefulness. Metabolic rate during sleep at thermoneutrality in day and night experiments was 0.24 to 0.31 Watts lower than that in quiet wakefulness. At low temperature this difference between sleep and quiet wakefulness during day and night experiments was 0.41 to 0.54 Watts. In both cold and thermoneutral conditions, however, there was a similar decrease of approximately 8% in

metabolic rate during sleep in comparison to quiet wakefulness.

Discussion

Sleep postures observed in the little penguin are similar to those seen in other penguin species although the little penguin, like the Galapagos penguin, was not observed to sleep with the bill tucked behind one of the flippers (Boersma 1976; Murphy 1936; Spurr 1975; Van Zinderen Bakker 1971; Wilson 1907). Since penguins often sleep upright, and even when lying down hold their heads above the ground, it is perhaps not unexpected that muscle tone is not decreased in the neck muscles during SWS.

Polygraphic indices of sleep and wakefulness in the little penguin correspond to the general avian pattern (Goodman 1974; Ookawa 1972). However, the presence of slow wave EEG activity during behavioural quiescence differs from the classic mammalian pattern of a desynchronized EEG during wakefulness. Such intrusion of slow waves has been reported in almost all avian polygraphic studies (Ookawa 1972) and hence may be considered typical of the avian EEG.

Sleep patterns

The proportion of PS (16.2% of TST) in the little penguin is much higher than the value normally given for birds, approximately 7% of TST (Goodman 1974). Data for the proportion of PS in mammals, however, are very variable and range from approximately 5 to 46% of TST (Zepelin and Rechtschaffen 1974). The increased amount of PS in the little penguin may be related to susceptibility to predation, one of the factors which is correlated with PS patterns in mammals (Allison and Cicchetti 1976). Little penguins nest in burrows and may not be as exposed as many birds, although

the burrowing owl has a PS component of only 5% of TST (Berger and Walker 1972).

Although sleep parameters in this study were recorded from four-hour experiments rather than 24 h periods, it appears that sleep patterns of little penguins are more evenly distributed between day and night than in many birds (Tymicz et al. 1975; Walker and Berger 1972). The lower proportion of sleep at night does not appear to be due to lack of acclimation to recording conditions since penguins also showed increased sleep time during the day when compared to the general avian pattern. This difference may also be related to predatory danger as the burrowing owl has considerable amounts of sleep during the activity phase of its circadian rhythm (Berger and Walker 1972). Conversely, although feeding at sea during the day, little penguins do not appear to be completely diurnal in their activity patterns since considerable social activity occurs at night around their burrows (Warham 1958).

King and gentoo penguins come ashore after feeding trips during the late afternoon and return to the sea at first light (Stonehouse 1960; Van Zinderen Bakker 1971). In the continuous daylight of the Antarctic summer nesting Adelle penguins show no single period of rest, but are active throughout the 24 h (Spurr 1978). However, when not breeding or moulting, many penguin species spend three to four months at a time at sea (Stonehouse 1967). Penguins at sea may employ both nocturnal and diurnal feeding patterns since krill (associated with squid and fish) rise to the surface at night (C.R. Brown, personal communication; Croxall and Prince 1980). Little penguins in southern Tasmania disperse from their rookeries after breeding and moulting (Hodgson 1975). If little penguins sleep at sea during this time, then sleep patterns may reflect those seen in cold air temperatures rather than at thermoneutrality due to the thermal load of immersion (Stahel and Nicol 1982).

The decrease in total sleep time observed with acute exposure to cold in the little penguin agrees with studies on cats (Parmeggiani and Rabini 1970) and rodents (Sakaguchi et al. 1979; Schmidek et al. 1972). By contrast, chronic exposure to cold in one ringed turtle dove resulted in an increase in total sleep time (Walker et al. 1981). The ringed turtle dove, however, exhibits shallow torpor and hence may preserve normal sleep patterns in response to cold stress, as has been found in mammalian hibernators (Haskell et al. 1979; Walker et al. 1983).

Contrary to the mammalian pattern in which

the decrease in sleep time appears to be predominantly due to a decrease in the proportion of PS, the duration of PS episodes and the ratio of PS to SWS in penguins remained relatively constant in cold compared to thermoneutral temperatures. Sakaguchi et al. (1979) concluded that the decrease in PS in cold exposed kangaroo rats is the result of a decrease in the number of transitions from SWS to PS due to both altered central thermoregulatory drive and cold peripheral stimuli.

The lack of selective reduction in PS with cold exposure in the little penguin may be due to the very short duration of PS episodes. Thermoregulation is severely suppressed during paradoxical sleep in mammals (Heller and Glotzbach 1977; Parmeggiani 1980) and birds (Graf et al. 1980). The short duration of PS characteristic of birds suggests that there is little chance for body temperature to drift in these periods and hence it would be unnecessary to differentially control SWS and PS in response to cold stimuli.

Cold exposure in pigeons at night results in a ratio of PS to TST of 10% (Graf et al. 1983), a value similar to the proportion of 7% of TST that pigeons spent in PS in normative sleep studies (Van Twyver and Allison 1972; Walker and Berger 1972). However, when body temperature is drastically lowered with spinal warming, the proportion of PS is reduced to about 2% of TST (Graf et al. 1983). Similarly, during shallow torpor in the ring necked dove, PS is successively reduced concomitant with a decrease in feathered skin temperature (Walker et al. 1981). Such results indicate that during hypothermia there does appear to be an association between peripheral cold stimuli and the amount of PS although this would not be expressed in normal conditions.

Metabolic rate

The variation in metabolic rate between day and night experiments was not simply the result of sleep. In awake birds at thermoneutrality there was still a difference in metabolism (0.4 Watts) between day and night although the prevalence of sleep at night accentuates this difference. Aschoff (1982) recently provided a predictive equation for the range in circadian oscillation of metabolism with weight in birds. A hypothetical one kilogram bird would be expected to decrease its resting metabolic rate at thermoneutrality by 0.7 Watts between day and night (units converted from original report), a difference almost twice that found between wakefulness during day and night in this study. If it is argued that data from birds at night in Aschoff's

compilation were likely to represent sleep, then comparing the difference between wakefulness during the day and sleep at night in the little penguin gave a value of 0.68 Watts which is similar to the empirical prediction.

There have been few studies which have directly investigated metabolic heat production and sleep in birds. Larochelle et al. (1982) found that black vultures sleeping with their head under a wing at relatively low air temperature (10 °C) had a lower heat production than awake birds at this temperature. This difference was ascribed by the authors to reduction of surface area by postural adjustments. At higher ambient temperatures this type of sleep posture would, in addition, reduce respiratory evaporative heat loss since inspired air temperature would be increased in relation to ambient and the birds would be rebreathing air of higher moisture content (Grant and Whittow 1983). In general terms, species (primarily mammalian) which have a relaxed sleeping posture would also decrease metabolism as the result of a decrease in muscle postural activity from that seen in quiet wakefulness (for example Jacobsen et al. 1964). Since the sleep posture of the little penguin in these experiments was not greatly different from that seen during quiet wakefulness, it is unlikely that the decrease in metabolic rate during sleep was due to postural changes.

In addition to behavioural means of heat conservation, thermal manipulation of the hypothalamus in small mammals has shown that autonomic thermoregulatory responses decrease during sleep (Heller and Glotzbach 1977). In birds extracerebral thermal receptors, particularly in the spinal cord, provide the dominant feedback loop for control of thermoregulation (Simon et al. 1976; see also an extensive review by Necker 1981). Cooling the spinal cord of pigeons demonstrated a decrease in the threshold for metabolic heat production during sleep (Graf et al. 1980). The similar suppression of metabolic rate during sleep in the little penguin in day and night experiments at different temperatures suggests that sleep represents a constant decrease in the set point for thermoregulation.

Energetic significance of sleep

It has been proposed that one of the major functions of sleep is to conserve energy (Allison and Van Twyver 1970; Berger 1975; Snyder 1966; Walker and Berger 1980). Evidence for this view, however, is mainly based on indirect arguments such as the presumed absence of sleep in ectotherms, appearance of sleep coincident with ho-

meothermy in young animals, correlation between sleep time and body size, and hibernation as an extension of SWS (Walker and Berger 1980; Zeppelin and Rechtschaffen 1974).

Suppression of thermoregulatory responses during sleep can also be viewed as an energy conserving mechanism. However, there are relatively few studies which have measured metabolic rate during sleep in comparison to quiet wakefulness without thermal manipulation of the central nervous system. Unfortunately, many papers are variously complicated by circadian effects, and the lack of data for quiet wakefulness or activity during wakefulness (Brebbia and Altschuler 1965; Haskell et al. 1981; Passmore and Durnin 1955; Roussel and Bittel 1979; Webb and Hiestand 1975).

The effect of sleep on nocturnal energy expenditure in sheep at thermoneutrality was examined by Toutain et al. (1977). Metabolic rate decreased by approximately 10% between sheep lying awake and during SWS and PS. However, when the decrease in metabolic rate during sleep is related to total daily sleep duration, Toutain et al. concluded that the direct effect of sleep on energy expenditure was less than 2%. Passmore and Durnin (1955) suggested that sleep in fasting man is associated with a decrease in approximately 7% but also noted that this is a very small proportion of daily energy expenditure.

A similar argument can be applied in this study to the sleep related decrease in metabolic rate and amount of sleep in the little penguin. Assuming a 12L:12D light cycle and that sleep patterns and metabolic rates in this study are representative of this hypothetical circadian rhythm, then it can be calculated from Fig. 3 and Table 1 that a resting awake little penguin at thermoneutrality would expend ca. 330 kJ/day. If this bird did not sleep at all, energy expenditure would increase by 2.4% compared to the normal value. Conversely, if the penguin spent all its time asleep, daily energy costs would be 4.7% less than the normal value.

Although the ubiquity of sleep implies that it provides some essential (albeit unknown) functions, this simplistic model suggests that the reduction in metabolic rate with sleep represents only a marginal suppression in overall energy expenditure of a resting penguin at thermoneutrality. There is even less chance for sleep to conserve energy in cold conditions since total sleep is much less than at thermoneutrality. Moreover, applying the same reasoning as above to the influence of the circadian rhythm, assuming sleep times remain unchanged but where metabolic rate is expressed for

day-time values only, there would be an increase in daily energy cost of 5.3% with respect to the normal value. The increment in metabolism upon hypothetical abolition of the circadian rhythm would be approximately twice that seen with the loss of sleep.

In general terms sleep-associated energy savings primarily depend upon total sleep time which must be balanced against the costs of not expending time and energy on other variables in the energy budget. Such energy savings may be of more proximate importance in birds that spend most of the rest phase of their diurnal cycle asleep when there is little opportunity to forage. Further, during periods of enforced starvation sleep may extend limited energy reserves (Walker et al. 1981). In this context sleep is greatly enhanced during the moult-fast of the Little Penguin where energetic demands are met by previously stored fat reserves (Stahel, unpublished observations).

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