© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb182634. doi:10.1242/jeb.182634

RESEARCH ARTICLE

The low-down on sleeping down low: pigeons shift to lighter forms of sleep when sleeping near the ground

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ABSTRACT

Sleep in birds is composed of two distinct sub-states, remarkably similar to mammalian slow-wave sleep (SWS) and rapid eye movement (REM) sleep. However, it is unclear whether all aspects of mammalian sleep are present in birds. We examined whether birds suppress REM sleep in response to changes in sleeping conditions that presumably evoke an increase in perceived predation risk, as observed previously in rodents. Although pigeons sometimes sleep on the ground, they prefer to sleep on elevated perches at night, probably to avoid nocturnal mammalian ground predators. Few studies to date have investigated how roosting sites affect sleep architecture. We compared sleep in captive pigeons on days with and without access to high perches. On the first (baseline) day, low and high perches were available; on the second day, the high perches were removed; and on the third (recovery) day, the high perches were returned. The total time spent sleeping did not vary significantly between conditions; however, the time spent in REM sleep declined on the low-perch night and increased above baseline when the pigeons slept on the high perch during the recovery night. Although the amount of SWS did not vary significantly between conditions, SWS intensity was lower on the low-perch night, particularly early in the night. The similarity of these responses between birds and mammals suggests that REM sleep is influenced by at least some ecological factors in a similar manner in both groups of animals.

KEY WORDS: Predation, Rapid eye movement sleep, REM sleep, Sleep site, Slow-wave sleep, SWS

INTRODUCTION

Although sleep constitutes roughly one-third of an average human's life, the basic function(s) of this state are still a subject of debate (Joiner, 2016; Peever and Fuller, 2017). Sleep as a behavioral state is characterized by reduced responsiveness to external stimuli, a species-specific posture and rapid reversibility to wakefulness (Meddis, 1975). Interestingly, in birds and mammals, sleep can be further divided into two distinct sleep sub-states, slow-wave sleep (SWS) and rapid eye movement (REM) sleep, based on changes in electroencephalogram (EEG) activity, muscle tone and eye movements (Lesku and Rattenborg, 2014). SWS is characterized by high-amplitude, low-frequency EEG activity with elevated spectral density in the 0.5–4.5 Hz frequency range, referred to as slow-wave activity (SWA) (Steriade et al., 1993; Rattenborg et al., 2011). REM sleep is characterized by low-amplitude, high-frequency EEG activity similar to the patterns occurring during wakefulness. Unlike wakefulness, REM sleep is accompanied by reduced muscle tone and intermittent myoclonic twitching, including rapid eye movements (Siegel, 2016). In birds, the reduction in muscle tone causes the head to drop to varying degrees (Dewasmes et al., 1985; Lesku et al., 2011a). Several aspects of SWS and REM sleep regulation are also similar in mammals and birds (Rattenborg et al., 2009).

Sleep regulation has been most extensively studied in mammals. During natural sleep and following sleep deprivation, EEG SWA during SWS increases as a function of prior time spent awake and decreases as a function of time spent asleep (Borbély et al., 1984; Rattenborg et al., 2009; Tobler, 2011). As arousal thresholds are positively correlated with the amount of SWA during SWS (Neckelmann and Ursin, 1993), this suggests that SWS-related SWA reflects the intensity of homeostatically regulated sleep processes. In addition to increased SWA, the compensatory response to extended periods of wakefulness can also result in increased time spent in SWS. The combined effect on SWA and time spent in SWS is expressed as slow-wave energy (the cumulative SWS-related SWA for a given period of time) (Leemburg et al., 2010). The time spent in REM sleep also increases following sleep deprivation (Borbély et al., 1984; Tobler, 2011), although, unlike SWS, it is unclear whether REM sleep has an intensity dimension.

In birds, similar responses to sleep deprivation can be observed (Rattenborg et al., 2009; Lesku et al., 2011b). Following short-term sleep deprivation, SWA during recovery SWS increases above baseline levels in pigeons (*Columba livia*; Martinez-Gonzalez et al., 2008; Lesku et al., 2011b) and white-crowned sparrows (*Zonotrichia leucophrys*; Jones et al., 2008). SWA is also higher in male pectoral sandpipers (*Calidris melanotos*) that sleep less during the breeding season (Lesku et al., 2012), and increases in great frigatebirds (*Fregata minor*) following foraging-induced sleep loss in the wild (Rattenborg et al., 2016). The time spent in REM sleep also increases in pigeons following short- and long-term sleep deprivation (Tobler and Borbély, 1988; Martinez-Gonzalez et al., 2008; Newman et al., 2008). In addition to this homeostatic response, REM sleep is regulated in a similar manner during ontogeny in mammals and birds. In both groups, the amount of time spent in REM sleep is highest in young animals and decreases across early ontogeny until plateauing at adult, species-specific levels (Roffwarg et al., 1966; Jouvet-Mounier et al., 1970; Scriba et al., 2013). This ontogenetic pattern may suggest that REM sleep plays a similar role in development in the two groups.

In addition to sleep deprivation, sleep also responds to changing ecological circumstances. In rats (*Rattus norvegicus*), the onset of SWS was delayed and SWA during SWS was lower immediately

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Received 12 April 2018; Accepted 30 July 2018

Journal of Experimental Biology (2018) 221, jeb182634. doi:10.1242/jeb.182634

following a simulated predator encounter (Lesku et al., 2008). In addition, although REM sleep was initially suppressed, a compensatory increase in time spent in REM sleep was observed later in the night (Lesku et al., 2008). Similarly, rock hyraxes (*Procavia capensis*), highly social animals, suppress REM sleep when sleeping in isolation as compared with sleeping in the relative safety of a group (Gravett et al., 2017a). Likewise, fear conditioning using electric shock in mice resulted in a reduction in the time spent in REM sleep for several hours following the conditioning treatment; however, this effect on REM sleep was dampened when mice were provided the option to escape the shock (Sanford et al., 2003, 2010). Finally, during the first few days after being moved to a new enclosure, horses do not lie down (Ruckebusch, 1970; see also Williams et al., 2008), a posture associated with REM sleep (Ruckebusch, et al., 1970). Wild African elephants (*Loxodonta africana*) also forgo lying down for 3–4 days, possibly in response to ecological challenges (Gravett et al., 2017b; see also Schiffmann et al., 2018; Tobler, 1992). In contrast to mammals, it is unknown whether birds can selectively suppress REM sleep in response to changing ecological circumstances.

From an evolutionary standpoint, sleep is a baffling state. Not only are sleeping organisms not carrying out important activities (i.e. feeding, searching for a mate, guarding/rearing young, etc.) but also the increased arousal thresholds and decreased sensory awareness associated with sleep leave organisms particularly vulnerable to predation. Animals mitigate this heightened risk of predation by sleeping at favorable times, and in sleep sites that minimize the risk of exposure to predators (Lendrem, 1983; Ball, 1992; Lima et al., 2005, Lesku et al., 2006; Voirin et al., 2014). Some birds maintain partial environmental awareness when sleeping in dangerous situations, such as the edge of a group, by sleeping with one eye open and less deeply with the associated cerebral hemisphere (Rattenborg et al., 1999). Predation risk and sleep site exposure are both major predictors of sleep duration in birds and primates (Anderson, 1998, 2000; Lesku et al., 2006; Roth et al., 2006). In spite of the important roll sleep site selection plays in the mitigation of predation pressure, to date, few studies have experimentally investigated how sleeping site affects sleep architecture.

Many diurnal birds retreat to elevated sleeping perches, presumably to avoid nocturnal mammalian ground predators. Consequently, perch height may influence a bird's perceived risk of predation, and thereby their sleep. Previously, the lack of wireless EEG recording devices precluded studies of sleep in birds housed in large aviaries with varied perching sites. Using an EEG data logger, we assessed the effect that roost site height had on sleep architecture in captive pigeons. We predicted that pigeons sleeping closer to the ground, where mammalian predators might be active at night, would take longer to fall asleep at night, exhibit less deep and more asymmetric SWS (Rattenborg et al., 1999, 2001), and disproportionately suppress REM sleep (Lesku et al., 2008).

MATERIALS AND METHODS

Housing and care

Six adult pigeons (*Columba livia* Gmelin 1789) were kept indoors in a room maintained at 20°C on a 12 h photoperiod. Pigeons were housed in pairs, one male and one female, in stainless steel aviaries (length 200 cm, width 100 cm, height 200 cm). Experiments occurred in two groups, 4 months apart. Within each aviary, two high (height 170 cm) and two low (height 20 cm) wooden perches were provided. The wooden perches (20.5 cm in length by 4 cm in width) were attached perpendicular to the cage wall. Perches were placed across from one another near each end of the aviary. A perch could accommodate only one pigeon at a time. Additionally, each enclosure was fitted with infrared sensitive cameras to record the birds' behavior.

EEG electrode implantation

Anesthesia was induced using isoflurane (5% vaporized in 1.0 l min^{-1} O_2) and a surgical plane was maintained using a lower dose (1.5–2.0% vaporized in 1.0 l min^{-1} O_2). To detect sleep-related changes in brain activity, four EEG gold-plated, round-tipped (0.5 mm diameter) pin electrodes were implanted in a row: two electrodes over each hemisphere, with one over the mesopallium and one over the hyperpallium. As with other birds, the hyperpallium could be seen through the cranium, facilitating electrode placement. The row was centered over the midline, 11.0 mm anterior, with the hyperpallial and mesopallial holes 2.0 and 6.0 mm, respectively, on each side of the midline. Electrodes over a given hemisphere were referenced to a gold-plated, round-tipped (0.5 mm diameter) pin electrode placed on the ipsilateral cerebellum. The electrodes were attached to a connector mounted on the bird's head with dental acrylic. The pigeons were allowed a minimum of 1 week post-surgical period before recordings commenced.

EEG recording

The EEG was recorded at 100 Hz using a data logger (Neurologger 2A; www.vyssotski.ch/neurologger2) that also records 3D acceleration. This logger has been used extensively to record the EEG in birds (Vyssotski et al., 2009; Lesku et al., 2012; Scriba et al., 2013; Rattenborg et al., 2016; Tisdale et al., 2017). The logger, with batteries, weighed 3.6 g.

Recordings took place during 3 consecutive 24 h periods (see Fig. 1). The loggers were placed on the pigeons in the evening before lights out and the first night was considered a post-handling period that was not scored or analyzed. Beginning at lights-on following the post-handling night, the baseline (high-perch) day began. Both high and low perches were present. To keep the baseline, experimental and recovery days uniform, on the baseline day we entered the room just after the lights turned on and simulated manipulating the perches, as done on the subsequent days. On the second day (henceforth referred to as 'low-perch' day), just after the lights turned on, the high perches were removed for the next 24 h. On the third day (recovery), just after the lights turned on, the high perches were reinstated for the final 24 h period. In order to minimize the amount of weight carried by the pigeons in this study, the minimum battery size was chosen. In two of the pigeons, this resulted in only partial recovery nights being obtained (one quarter obtained in one pigeon and two full quarters obtained in the other pigeon). Full recovery nights were obtained from 4 of the 6 pigeons.

Scoring criteria

The recordings were scored for wake, SWS and REM sleep using 4 s epochs following Lesku et al. (2011b). Briefly, an epoch was categorized as SWS when it showed high-amplitude, slow waves and an absence of head movements in the accelerometry channels (see Fig. S1A,B). Epochs with activation were scored as wakefulness if they were associated with rapid head movements, as reflected by the accelerometer and/or video recordings (see Fig. S1A). Epochs with activation were scored as REM sleep if the head remained motionless, and the eyes remained closed. REM sleep was also associated in some cases with the slow falling of the head, as revealed in the accelerometry and video recordings (see Fig. S1B). Also, phasic twitching of the bill occasionally

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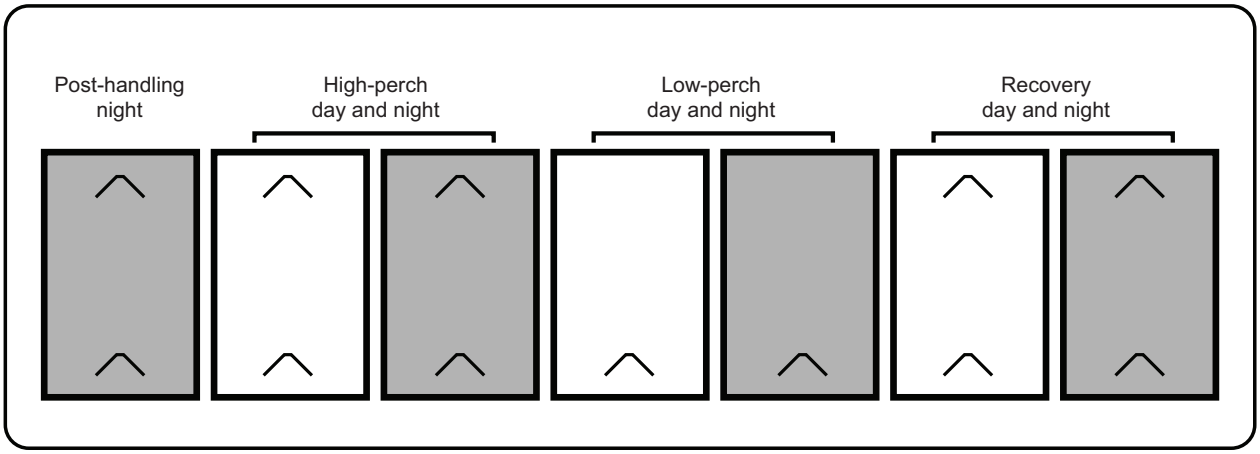

Fig. 1. Schematic diagram of the experimental protocol. Each rectangle shows the position of the perches (inverted 'V') on the cage wall during successive days (white) and nights (grey). To accommodate two pigeons, in each case, the opposing aviary wall had the same perch configuration.

occurred during REM sleep. Finally, large movements during active wakefulness (walking, feeding and scanning) were often associated with large artifacts in the EEG. Such epochs were scored as wakefulness despite the absence of detectable EEG activation.

Analysis

All recordings were visually scored using RemLogic (Natus; Embla RemLogic 3.4.0) for wake, SWS and REM sleep in 4 s epochs (see Lesku et al., 2011b). The recordings were also scored for the presence of artifact in any of the EEG signals.

For each state, all 4 s artifact-free epochs were analyzed with the fast Fourier transform (0.39 Hz bins) applied to Hamming-windowed data. Average SWS-related SWA (0.78–3.9 Hz power) and SWS-related slow-wave energy (SWE; sum of SWS-related SWA) were calculated separately for the total night and total day, as well as in 3 h time bins for each EEG channel across the multiday experimental period. Spectral data were normalized as a percentage of the mean power across all frequency bins for artifact-free periods of SWS occurring across the entire recording period. A SWA interhemispheric asymmetry index (L−R/L+R; L and R=SWA for the left and right hemispheres, respectively) (Rattenborg et al., 2016) was calculated for each artifact-free epoch of SWS.

For each state, we calculated the percentage of recording time, percentage of total sleep time, the number of bouts and average bout duration. A bout was defined as one or more successive epochs scored as the same state. For each bird, each variable was averaged over 3 h time bins. Analyses were done using the R (v3.4.2) statistical computing package. Models were structured including bird as a random factor and photoperiod and time bin as fixed factors. A best-fit model was first selected by testing model significance with an ANOVA and selecting the simplest significant model. Variables compared with these models were sleep state as a percentage of time period, number of episodes, average bout duration, SWA and SWE. Linear mixed-effects models were then fitted for each variable, using the selected best-fit model for each variable using the restricted maximum likelihood approach for estimating variance in the lmer function within the lme4 package for R (https://CRAN.R-project.org/package=lme4). If an interaction effect was present between time bins per photoperiod, further models were fitted including individual time bins as a fixed factor to pinpoint where this interaction was most pronounced. SWA and SWA interhemispheric asymmetry index were also averaged over 3 h time bins and analyzed using the same methods. Values reported in text are the mean±s.e.m. Time spent sleeping on high and low perches was scored across days. One of the pigeons, from which only a partial recovery night of EEG data was obtained, chose to sleep on the ground during the recovery night, even though a high perch was available. This partial night was thus excluded from the analysis. All other pigeons spent both baseline and recovery nights on high perches. The recording device on another pigeon stopped in the third quarter of the recovery night. The second half of this night is thus missing from the analysis for this bird. Statistics are only provided for results with *P*-values exceeding 0.05.

RESULTS

Roost usage

All but one pigeon used the high roosts when present during the night. This exception continued to sleep on the low perch on the recovery night, even though the high perch was reinstated. This pigeon was thus excluded from the analysis of the recovery night. During the daytime, pigeons spent the majority of their time on the ground. On the baseline and recovery days, when both low and high perches were available, pigeons spent the majority of their time down low (time spent on the ground or low perch on baseline day: 88.7±1.3%; high perch usage on baseline day: 11.3±1.3%; time spent on the ground or low perch on recovery day: 86.2±2.7%; high perch usage on recovery day: 13.8±2.4%). The pigeons spent relatively little time sleeping on the high perches during the daytime (sleep as a percentage of time on high perch on baseline day: 13.1±5.3%; sleep as a percentage of time on the ground or low perch on baseline day: 13.3±1.1%; sleep as a percentage of time on high perch on recovery day: 2.5±1.2%; sleep as a percentage of time on the ground or low perch on recovery day: 8.8±1.3%).

Influence of perch height on wakefulness and sleep

Wake

During the baseline period, the pigeons spent more time awake during the day than during the night (Fig. 2A; $P>0.001$). There was no significant difference between time awake on the low-perch night (percentage of night: 29.1±4.0; Fig. 2A), or the recovery night (percentage of night: 24.7±4.1), and baseline (percentage of night: 24.7±2.5). The amount of time spent awake decreased across the nights ($P=0.030$). Wake bout duration was significantly shorter on the low-perch night (39.8±5.5 s) as compared with the baseline night (59.6±8.7 s; $P<0.001$; Fig. 2B). The number of wake episodes increased between the baseline (188±16.3) and the low-perch night

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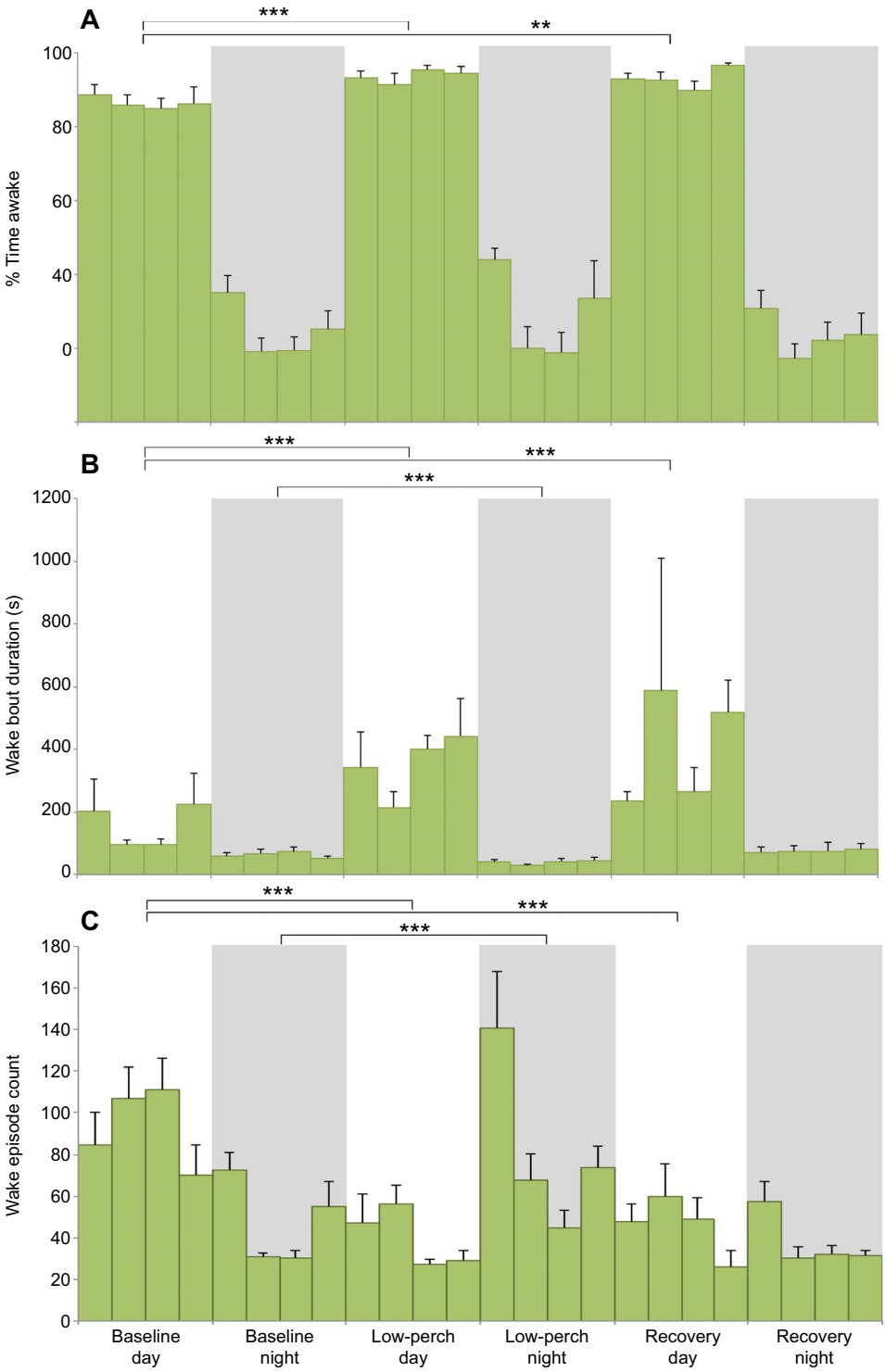

Fig. 2. Timing of wakefulness across the baseline, low-perch and recovery days. (A) Percentage time spent awake, (B) duration of bouts of wakefulness and (C) number of episodes of wakefulness. Values are means ±s.e.m. for each 3 h time bin. The gray shading indicates dark phases. Statistics were performed using the best-fit linear mixed model, fitted using the restricted maximum likelihood approach. Only statistically significant differences between photoperiods are reported. For interaction and time bin statistics, see Results. ***P<0.001 and **P<0.01.

(327±37.0; P<0.001; i.e. the sum of histogram bars during the night in Fig. 2C) and decreased across nights (P=0.001).

Time spent awake increased significantly compared with baseline (86.4±1.1%) on both the low-perch day (93.6±1.7%; P<0.001) and the recovery day (93.0±1.3%; P=0.001; see Fig. 2A). Changes in daytime wake were accompanied by an increase in wake bout duration between the baseline day (104.8 ±10.0 s) and the low-perch day (299.9±62.4 s; P<0.001) and between the baseline and recovery days (272.9±64.6 s; P<0.001; Fig. 2B). Wake bout duration also increased across time bins (P=0.038). Additionally, the number of episodes of wake decreased between the baseline day (372.2±35.6) and the low-perch day (159.7±24.5; P<0.001), as well as between the baseline and recovery days (182.3±33.1; P<0.001; Fig. 2C). The number of wake episodes also decreased across each day (P=0.031).

SWS

Under baseline conditions, SWS made up more of the night than the day (Fig. 3A; P>0.001). The time spent in SWS varied little both within and across nights (Fig. 3A). SWS bout duration

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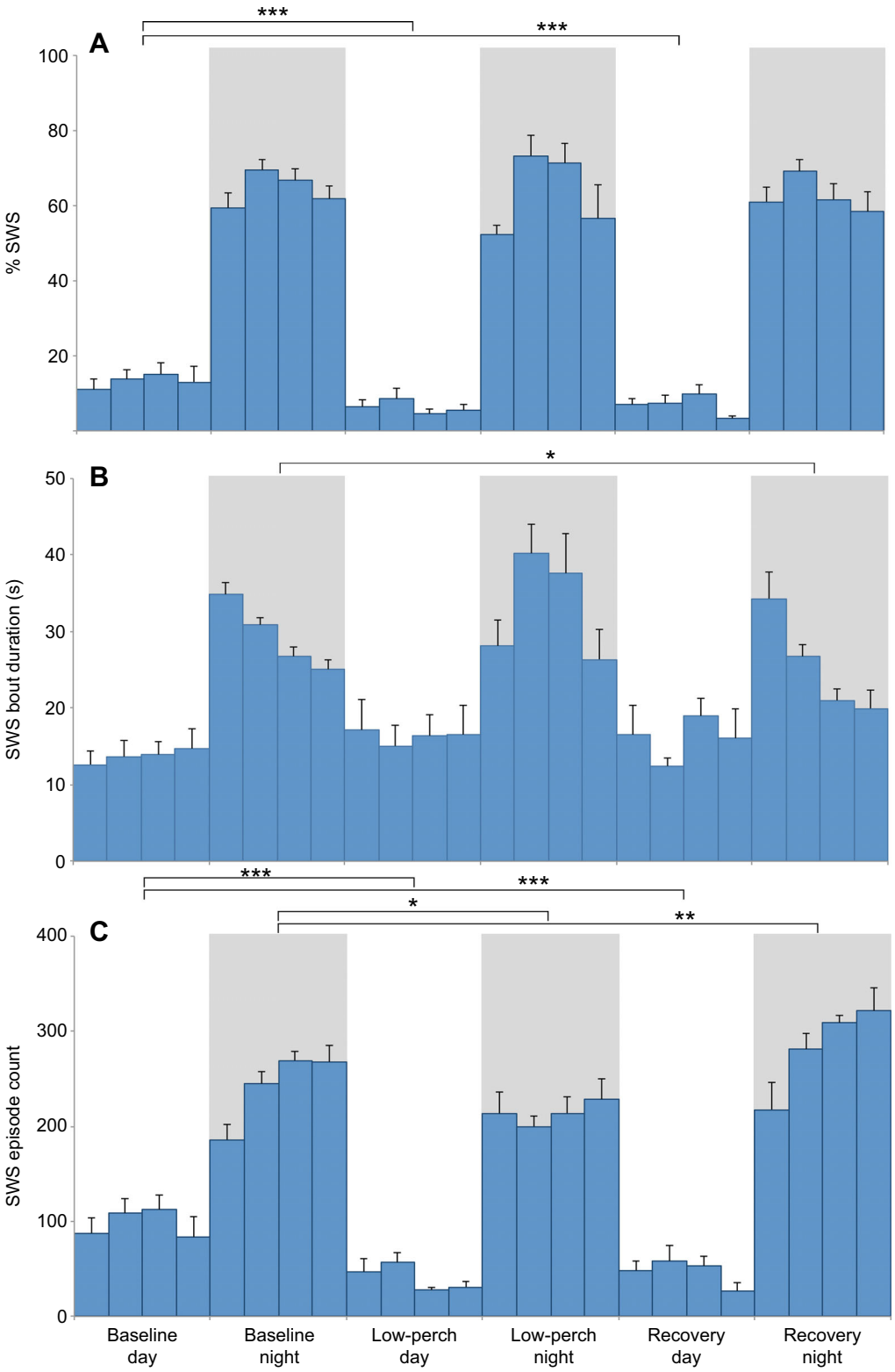

Fig. 3. Timing of slow-wave sleep (SWS) across the baseline, low-perch and recovery days. (A) Percentage time spent in SWS, (B) duration of bouts of SWS and (C) number of episodes of SWS. Values are means±s.e.m. for each 3 h time bin. The gray shading indicates dark phases. Statistics were performed using the best-fit linear mixed model, fitted using the restricted maximum likelihood approach. Only statistically significant differences between photoperiods are reported. For interaction and time bin statistics, see Results. ***P<0.001, **P<0.01 and *P<0.05.

decreased between the baseline (28.8±0.7 s) and recovery nights (24.6±1.3 s; P=0.025; Fig. 3B) and also decreased within nights (P<0.001). The number of SWS episodes decreased between the baseline (967.7±47.4) and low-perch nights (855.8±27.0; P=0.013), and increased between the baseline and recovery nights (1089.8±34.4; P=0.004). The number of episodes increased across each night (P<0.001; Fig. 3C).

The amount of SWS during the daytime on the low-perch (6.3±1.6%; P<0.001) and recovery day (6.9±1.3%; P<0.001) was lower than during the daytime on the baseline day (13.3±1.0%; Fig. 3A). SWS bout duration was unchanged across days (Fig. 3B). The number of SWS episodes decreased between the baseline day (391.3±38.0) and the low-perch day (163.0±27.0; P<0.001), and between the baseline day and the recovery day (186.7±34.4; P<0.001; Fig. 3C).

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REM sleep

Under baseline recording conditions, REM sleep occurred almost exclusively at night, and increased as the night progressed (Fig. 4A; $P<0.001$) due to an increase in the duration (Fig. 4B; $P<0.001$) and number (Fig. 4C; $P<0.001$) of bouts. The most pronounced effects on night-time sleep times were specific to REM sleep (Fig. 4A). REM sleep as a percentage of the recording period decreased between the baseline (10.9±0.7%) and low-perch night (7.5±1.0%; $P<0.001$), and increased between the baseline and recovery night (13.5±0.9%; $P=0.002$). The amount of REM sleep also increased within all nights across all conditions ($P<0.001$). Although REM sleep episode duration remained the same across nights (baseline: 6.0±0.2 s; low-perch: 5.9±0.2 s; recovery: 6.1±0.3 s; Fig. 4B), it showed a similar increase within all three nights ($P<0.001$; Fig. 4B). The number of REM sleep episodes was lowest on the low-perch night (536.8±54.7) compared with the baseline night (785.0±45.4: $P<0.001$; Fig. 4C). The number of REM sleep episodes increased significantly on the recovery night (955.5±60.3) when compared with the baseline night ($P=0.001$; Fig. 4C). The number of REM episodes also showed an increase within the night across all conditions ($P<0.001$; Fig. 4C).

REM sleep was consistently low during the light phase of the photoperiod during all days (Fig. 4A).

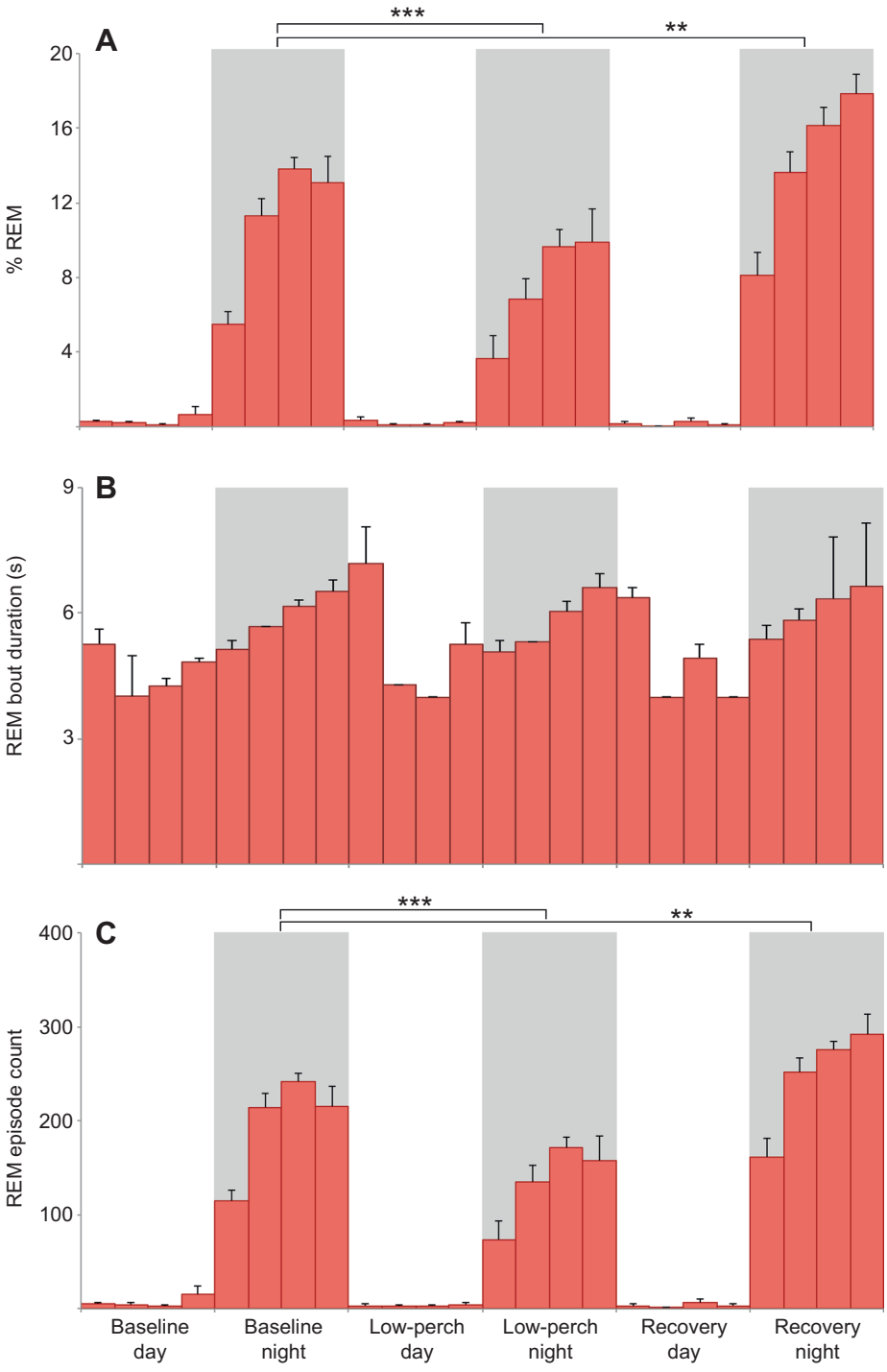

Fig. 4. Timing of rapid eye movement (REM) sleep across the baseline, low-perch and recovery days. (A) Percentage time spent in REM sleep, (B) duration of bouts of REM sleep and (C) number of episodes of REM sleep. Values are means±s.e.m. for each 3 h time bin. The gray shading indicates dark phases. Statistics were performed using the best-fit linear mixed model, fitted using the restricted maximum likelihood approach. Only statistically significant differences between photoperiods are reported. For interaction and time bin statistics, see Results. ***$P<0.001$ and **$P<0.01$.

SWA

SWS-related SWA also varied across nights (Fig. 5). SWA decreased significantly between the baseline (443.7±32.7%) and low-perch nights (417.0±33.1%; $P<0.001$). Although SWA did not vary significantly across time bins on the baseline and recovery nights, on the low-perch night there was a significant increase in SWA activity across the night ($P=0.006$). SWA was lowest in the first quarter of the low-perch night (369.1±32.7%) and increased across the night, peaking in the fourth quarter (439.5±30.9%) of the night. SWA during the first quarter of the low-perch night was significantly lower than that in the first quarter of the baseline night ($P<0.001$). SWA during the daytime was consistently elevated compared with that during the night-time. Average daytime SWA was higher during the low-perch day (568.9±37.5) than during the baseline day (504.6±31.1; $P<0.001$). SWA was not elevated on the recovery day (551.6±47.0; $P=0.085$) relative to the baseline day. SWE showed no changes between experimental conditions across days or nights.

SWA asymmetry

SWA was not statistically different between the left and right mesopallia. Conversely, SWA differences were significant across all conditions between channels overlying the hyperpallium (baseline day: $P=0.005$; baseline night: $P=0.002$; low-perch day: $P=0.008$; low-perch night: $P=0.004$; recovery day: $P<0.001$; recovery night: $P=0.023$). SWA in the right hemisphere of the hyperpallium was on average higher than that in the left hemisphere in all birds, suggesting a hemispheric bias in sleep intensity. The magnitude of this interhemispheric asymmetry index was not significantly different between experimental conditions.

DISCUSSION

Pigeons modulated various aspects of their sleep architecture in response to the height of available perches. When compared with that on the first high-perch (baseline) night, REM sleep decreased on the low-perch night and increased above baseline levels on the subsequent high-perch recovery night. In addition, on the low-perch night, SWS showed a significant decrease in SWA on the low-perch night as compared with baseline. This decrease in SWA was most pronounced in the first quarter of the low-perch night. These results parallel those observed in mammals presented with housing situations inducing a higher perceived risk of predation or following a simulated encounter with a predator (Lesku et al., 2008; Gravett et al., 2017a), providing further evidence that REM sleep and SWS share similar regulatory mechanisms in these taxonomic groups.

REM sleep is a paradoxical state that has been viewed as either a particularly dangerous sleep state or a protective sleep state. The wake-like neuronal activity observed during REM sleep led to the hypothesis that REM sleep serves a ‘sentinel’ function, such that if awoken from this state the organism would be more prepared to react as compared with arousal from SWS (Lima et al., 2005). Indeed, evoked potentials occurring in response to sensory stimulation during REM sleep are similar to those occurring during wakefulness, whereas evoked potentials were nearly absent during deep SWS, suggesting an increased ability to process sensory information during REM sleep as compared with deep SWS (Bastuji and García-Larrea, 1999; Nashida et al., 2000; Cote et al., 2001). Furthermore, immediately following arousal from REM sleep, animals show an increased state of alertness as compared with that following SWS (Horner et al., 1997). In addition, REM sleep is frequently associated with brief arousals, perhaps allowing animals to quickly and periodically assess their surroundings during sleep (Van Twyver and Garrett, 1972). In contradiction to this theory, arousal thresholds reported for REM sleep are often increased as compared with those for SWS (Dillon and Webb, 1965; Van Twyver and Garrett, 1972; Amlaner and McFarland, 1981; Neckelmann and Ursin, 1993). Also, our results suggest that rather than being a protective state, REM sleep is a particularly

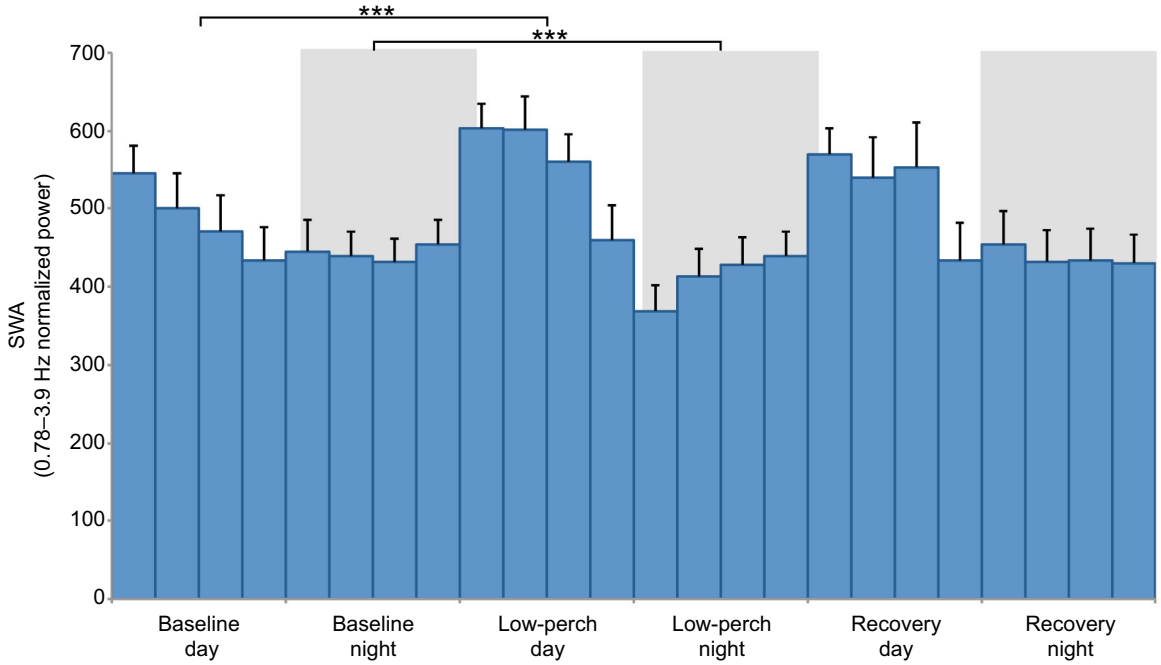

Fig. 5. Mean (±s.e.m.) normalized SWS-related slow-wave activity (SWA) for 3 h time bins across the 72 h experimental period. The dark phases are indicated by gray shading in each plot. Statistics were performed using the best-fit linear mixed model, fitted using the restricted maximum likelihood approach. Only statistically significant differences between photoperiods are reported. For interaction and time bin statistics, see Results. ***$P<0.001$.

dangerous state (Lima et al., 2005; Lesku et al., 2008, 2009). If REM sleep was serving a sentinel function, the amount of REM sleep would be expected to increase as a percentage of sleep time when birds slept on a lower perch that was more exposed to potential terrestrial nocturnal mammalian predators. Instead, we saw the opposite effect, with REM sleep decreasing when birds slept near or on the ground. This response is similar to that seen in rats following a simulated predatory event (Lesku et al., 2008) and in the social rock hyrax when forced to sleep in individual housing conditions (Gravett et al., 2017a). In addition, the amount of REM sleep increased above baseline levels on the high-perch, recovery night. The recovery of lost REM sleep when sleeping in a safe location is also inconsistent with the hypothesis that REM sleep is a protective state. Collectively, these findings indicate that REM sleep is a dangerous state that can be selectively reduced under risky ecological situations. Furthermore, the preservation of some REM sleep under such conditions indicates that REM sleep must serve an important function.

Although the time spent in SWS was similar across nights, SWS intensity was lowest on the low-perch night. This effect was primarily due to the suppression of SWS-related SWA in the first part of that night, after which SWA gradually increased toward baseline levels. This pattern suggests that the pigeons initially found the low perch to be particularly dangerous and therefore suppressed SWS intensity. The subsequent increase in SWA toward baseline levels may reflect the outcome of competing processes, i.e. the persistent perception of predatory risk suppressing SWA and the homeostatic pressure increasing SWA. SWS bout duration decreased on the final night and showed a decreasing trend within nights. This is reflective of the increasing trend in REM sleep occurrence and bout duration within nights, particularly on the recovery night when the amount of REM sleep was higher compared with baseline. Finally, although pigeons did sleep more deeply (based on SWA) with the right hyperpallium, the intensity of this asymmetry did not vary between conditions.

As for night-time sleep, daytime sleep was also influenced by the availability of high perches. The time spent sleeping decreased during the low-perch day, as a result of longer wake bouts and fewer SWS bouts. SWA was higher overall on the low-perch day as compared with the baseline day. These results suggest that perhaps in order to maintain a higher level of vigilance during the light on day 2, the pigeons consolidated their daytime sleep into infrequent but particularly intense bouts of SWS, an anti-predation strategy predicted by mathematical modeling (Lima et al., 2005; Lima and Rattenborg, 2007). Indeed, SWE did not vary between days, suggesting that in spite of sleeping less on the low-perch day, the pigeons had a similar discharge of homeostatic sleep pressure on all days. The reasons why the pigeons did not employ this strategy on the low-perch night are unclear, but might reflect different strategies for dealing with daytime and night-time predators. In general support of the idea that the pigeons employ time of day-dependent sleep strategies is the fact that even when high perches were available, the birds showed a preference for sleeping on the ground in the daytime. Finally, the changes in sleep observed during the low-perch day persisted on the recovery day, even though the high perches were available. Perhaps the alteration to the housing conditions itself (the removal and then replacement of the high perches) presented enough of a novel situation to trigger a heightened level of vigilance during the days following these alterations. It is also conceivable that increased perception of predatory risk induced by the low-perch night persisted even after the higher perch was reinstated.

Sleeping animals have a lessened ability to detect and react to the presence of a predator, making sleep a risky state. In spite of this risk, most animals devote a relatively large amount of time to this state instead of performing tasks actively contributing to their evolutionary fitness, such as feeding. Despite the ability to mitigate the risk from predation while sleeping by selecting protected or elevated sleeping sites, the risk from predation during sleep was likely an important evolutionary constraint on the evolution of longer sleeping times (Lesku et al., 2006, 2009). The greater time devoted to sleep, regardless of this trade-off, hints at the importance of the function or functions being carried out during sleep. Because predation likely played an important role in the evolution of sleep, it is possible that studying the impact of predation pressure on sleep patterns could also shed light on the functional aspects of sleep and the regulatory mechanisms underlying the different sleep states.

In addition to the evolutionary and functional implications of this study, these results also have implications for the design of bird housing. Our results demonstrate that perch height can have a substantial impact on the sleep patterns of birds, which primarily manifests in a suppression of REM sleep. However, given the short-term nature of our study, we cannot determine whether the observed changes in sleep would persist in birds chronically housed with only a low perch or in the lower rows of cage racks. Nonetheless, our findings raise the possibility that sleep remains altered under such conditions. As sleep interacts with various cognitive and physiological processes (Fishbein, 1971; Benca et al., 1989; Spiegel et al., 1999; McEwen, 2006), our findings suggest that cage height should be taken into consideration when designing experiments and analyzing data from captive birds.

Conclusions

Sleep in birds resembles sleep in mammals in many ways. In this study, as in mammals, pigeons sacrificed a significant amount of REM sleep when they apparently perceived an increase in the risk of predation. On the recovery night, the pigeons then showed a rebound in the amount of REM sleep. These similar responses suggest that the mechanisms underlying the regulation of REM sleep are shared by birds and mammals.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: R.K.T., J.A.L., N.C.R.; Methodology: R.K.T., J.A.L., N.C.R.; Software: G.J.B.; Formal analysis: R.K.T., J.A.L., G.J.B., N.C.R.; Investigation: R.K.T., J.A.L.; Resources: A.L.V.; Writing - original draft: R.K.T., N.C.R.; Writing - review & editing: R.K.T., J.A.L., G.J.B., A.L.V., N.C.R.; Visualization: R.K.T.; Supervision: N.C.R.

Funding

This project was funded by the Max-Planck-Institut für Ornithologie. G.J.L.B. is part of the Consortium on Individual Development (CID), which is funded through the Gravitation Program of the Dutch Ministry of Education, Culture and Science (Ministerie van Onderwijs, Cultuur en Wetenschappen) and the Netherlands Organization for Scientific Research (Nederlandse Organisatie voor Wetenschappelijk Onderzoek, NWO; grant number 024.001.003). J.A.L. was supported by the Australian Research Council (DP170101003).

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.182634.supplemental

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