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Opinion

The sociality of sleep in animal groups

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Group-living animals sleep together, yet most research treats sleep as an individual process. Here, we argue that social interactions during the sleep period contribute in important, but largely overlooked, ways to animal groups' social dynamics, while patterns of social interaction and the structure of social connections within animal groups play important, but poorly understood, roles in shaping sleep behavior. Leveraging field-appropriate methods, such as direct and video-based observation, and increasingly common on-animal motion sensors (e.g., accelerometers), behavioral indicators can be tracked to measure sleep in multiple individuals in a group of animals simultaneously. Sleep proximity networks and sleep timing networks can then be used to investigate the collective dynamics of sleep in wild group-living animals.

Sleeping in groups

Sleep is a seemingly ubiquitous and remarkably variable biological process with substantial differences in architecture, duration, and neurophysiology within and between species [1–4]. How and why animals sleep in such diverse ways remains a mystery. As the ongoing revolution in wearable technology makes it easier to measure sleep in the wild [5–7], it is becoming clear that animals' sleep patterns are strongly shaped by the selection pressures imposed by their ecologies [6]. For instance, sleep in natural settings can be of different duration compared with sleep in captivity [8,9] and can even shift from being diurnal to nocturnal [10,11]. However, most studies treat sleep as an individual process, even though many animals sleep in groups (e.g., [12,13]). Here, we argue that to understand the functional significance of the variation that we observe in natural sleep patterns, sleep research must consider not only the effects of the physical environment in which sleep occurs [2,14,15] but also the effects of the social environment.

There is mounting evidence that social factors play a fundamental role in shaping sleep patterns. Social stimuli can entrain the sleep–wake rhythms of an individual to that of the whole group [16], for example, substrate-propagated vibrations synchronize circadian rhythms in honey bees (*Apis mellifera*) [17]. Social entrainment in meerkats (*Suricata suricatta*) gives rise to group-specific sleep ‘traditions’ where neighboring groups show differences in sleep timing that persist through generations despite complete turnover in group membership [18]. Sleep duration can be affected by social relationships [19] and social context [20]. For example, olive baboons (*Papio anubis*) sleep less when the number of group members in their local environment increases [20], and bumble bees (*Bombus terrestris*) suppress sleep in the presence of offspring [21]. Mating strategies also influence sleep. Male pectoral sandpipers (*Calidris melanotos*) suppress sleep for weeks during the mating season [22], male fruit flies (*Drosophila melanogaster*) lose sleep when paired with females (reviewed in [23]), and male antechinus (*Antechinus swainsonii* and *A. agilis*) reduce sleep during the breeding season [24]. Female mallards (*Anas platyrhynchos*) decrease their rates of vigilance as the number of

Highlights

Animals that live in groups do not sleep in isolation.

Research has largely divorced the study of sleep from this social context, focusing on individuals sleeping alone in laboratory settings.

Technological advances now make it possible to quantify the sleep behavior of many animal species in socially relevant field contexts, opening a new research frontier: the social dynamics of sleep.

Research on the social dynamics of sleep promises to reveal critical, yet underappreciated, feedback between sleep and structure in animal societies.

By treating sleep as a collective phenomenon, we propose a new framework that leverages simultaneous monitoring of the sleep of members of social groups, combined with time-series and social network analyses, to investigate how the social environment shapes (and is shaped by) sleep.

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males (who display elevated rates of vigilance and are at higher risk of detection by predators owing to their brightly colored breeding plumage) in the sleeping flock increases [25]. Sleep is often organized into discrete stages that are characterized by different electrophysiological signatures and that are thought to serve different functions for the animal [26]. Two examples of sleep stages are rapid eye movement (REM) sleep and non-REM sleep, observed in terrestrial mammals [27] and birds [28]. REM sleep is marked by random eye movement, loss of muscle tone, and low-amplitude, high-frequency (6–10 Hz) waves in the electroencephalogram, while non-REM sleep is marked by high-amplitude, low-frequency (<4 Hz) waves in the electroencephalogram [29]. Social interactions can alter sleep organization indirectly through their impact on individuals' physiology. For example, stress associated with social defeat increases sleep intensity in rats (*Rattus norvegicus*, strain Tryon Maze Dull S3) during non-REM sleep [30]. Social defeat in laboratory mice (*Mus musculus*, strain C57BL/6J) increases the duration of non-REM sleep and, depending on the number of aggressive encounters, that of REM sleep as well [31]. Sociality also influences sleep neurophysiology; for example, in cohoused laboratory mice, sleeping with conspecifics fragments non-REM sleep in individuals but can synchronize the timing of REM sleep across individuals [32].

Why do animals sleep in groups? Animals might accrue a variety of benefits from sleeping socially, including improved selection of secure sleeping sites through social decision-making [12], reduced predation risk through dilution [33], presence of conspecific sentinels [6,34], increased mating opportunities [35], energy savings through social thermoregulation [36], and information exchange [37,38]. A group of sleeping animals consists of individuals that share behavioral goals in a common environment that is subject to shared external stimuli and temporal structure (Figure 1). Heterogeneity in

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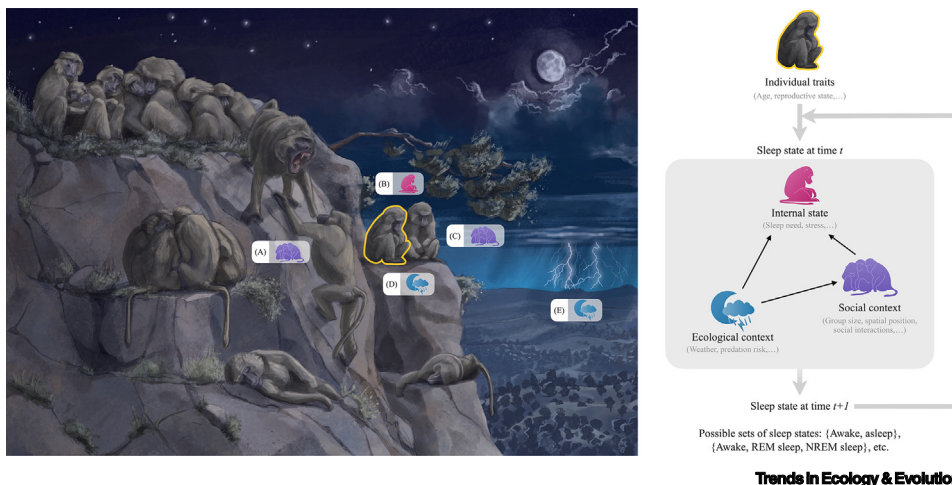


Figure 1. The interplay of sleep and sociality in wild animal groups. Social sleep occurs in dynamic, spatially heterogeneous conditions. A tendency for synchronized sleep [20] (and therefore limited sentinel vigilance during the sleeping period [68]) may lead groups to seek remote sleeping sites such as steep cliff walls away from predators. Sleeping in larger groups may lead to greater sleep disturbance by others in the group (A) and less sleep, while cold and rainy conditions may lead to competition for favorable spatial positions at the sleep site. The observed sleep pattern of an individual (yellow silhouette) can be considered to be the outcome of how the individual's internal state (B: sleep need [69], stress, etc.) interacts with social context (C: group size, spatial proximity to others, nearest neighbors, etc.) and ecological context (D: spatial position within sleep site, risk of predation or falling; E: exposure to inclement weather, etc.). Interactions between an individual's internal state, social context, and environmental context will be modulated by individual traits (e.g., age, sex, rank, reproductive state, etc.) to yield the observed temporal progression of sleep states. Illustration of the sleeping troop of olive baboons (*Papio anubis*) by Javier Lázaro.

individual, social, and spatial factors will interact to produce differences in individual sleep patterns as well as degree of sleep-state synchronization between individuals, which, when combined, may lead to emergent patterns of group sleep. The interface of sleep and sociality thus poses a profusion of new questions at multiple levels of social organization. Here, we articulate some of these research questions, propose analytical tools to facilitate social sleep research (Figure 2), and synthesize the sleep measurement literature to highlight the opportunities (and discuss the caveats) of using emerging technological innovations to quantify social sleep in the wild.

Research at the interface of sleep and sociality

Broadly speaking, the interface between sleep and sociality has three main facets: (i) how individual sleep varies with social traits (e.g., dominance rank), (ii) how individual sleep varies with group-level traits (e.g., group size), and (iii) if and how coupling of sleep states between individuals takes place and whether this leads to the emergence of aggregate group-level sleep patterns. The questions that we outline in the following sections explore these facets in more depth. Where possible with the current state of knowledge, we situate these questions within an eco-evolutionary framework.

How does an individual's social traits influence their sleep?

In many animal species, social phenotypes are heterogeneous, and traits such as dominance rank [39,40], social centrality, and affiliative and kin relationships are expected to affect sleep patterns. Social traits can have both direct and indirect effects on sleep behavior; low-ranking individuals, for example, may experience social exclusion from favorable spatial locations at the sleep site that increase their exposure to conditions (e.g., inclement weather and predators) that disrupt sleep (reviewed in [40]; Figure 1). Mallards at the edge of a sleeping group, for example, spend more time sleeping with one half of their brain while being vigilant for predators with the other half (termed unihemispheric sleep) than individuals near the group's center [41], and sleep in chinstrap penguins (*Pygoscelis antarcticus*) is likely influenced by trade-offs between increased predation risk at the periphery of nesting colonies and aggressive social interactions near the center [4]. At the same time, individual sleep also influences social traits. For example, a recent study on humans found that deeper sleep in regions of the brain that are positively related to prosociality was associated with increased prosocial preferences [42]. It is plausible that individuals who get sufficient sleep experience cognitive benefits such as improved attention, working memory, and visuomotor performance [43,44] that enable them to build stronger affiliative relationships or compete more effectively, thereby increasing their dominance rank. Investigating the bidirectional links between sleep patterns and social traits can help to illuminate how the costs and benefits of social sleeping are realized differently across individuals in the group.

How do group-level traits influence individual sleep?

For gregarious species, key aspects of the social environment, including group size, demographic composition, and degree of cohesion, are expected to influence individual sleep. Sleeping in larger groups offers conditions that could improve sleep (e.g., lower predation risk and greater number of sentinels) but also those that could worsen sleep (e.g., through greater sleep disturbance by others in the group). In Japanese macaques (*Macaca fuscata yakui*), for example, wakefulness of one individual often disturbs the sleep of other members of the sleeping huddle, particularly in huddles that are comprised of unrelated individuals [19]. Such trade-offs can lead to 'dome-shaped' curves of sleep duration versus group size, as documented in gulls (*Larus* sp.), where the percentage of time spent sleeping by individuals increases until flock size is around 60 and then decreases [45]. It is also likely that key aspects

of group behavior, including coordination, decision-making, and cooperative potential, will be influenced by the sleep of its members. For example, sleep loss in honey bees reduces waggle dance precision, which is expected to decrease the followers' flight accuracy [46]. This has potential fitness consequences due to less efficient recruitment to a quality food source [47]. Cross-group and cross-population comparisons are needed to shed light on how variability in group-level traits maps onto the sleep of group members and how variation in sleep patterns (e.g., duration and fragmentation) impacts the structure and functioning of animal societies. Comparisons of similar-sized sleeping groups across species will yield important insights into how sociality mediates between ecological pressures and the physiological need to sleep (Figure 1, right) [14,20,34].

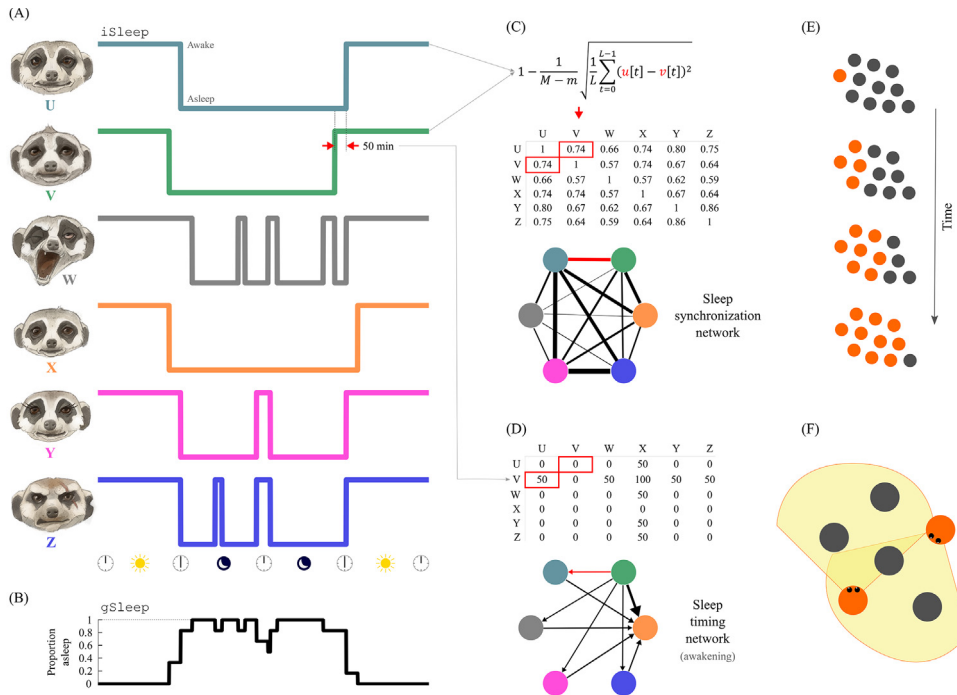
Does sleep become coupled in socially sleeping individuals, and does this lead to the emergence of collective dynamics in group-sleep behavior?

Behavioral contingency at the individual level (i.e., copying others' sleep/wake state) can lead to waves of sleep or vigilance at the group level (Figure 2E) [48]. Conversely, individuals can maximize their combined antipredator vigilance by adopting the opposite of others' sleep/wake state, leading to asynchronous sleep patterns at the group level [34]. In addition to empirical studies, modeling approaches inspired from the field of collective behavior [49] can help to explore the kinds of collective sleep behaviors that could theoretically arise, for instance, by varying 'rules' that determine why an individual awakens (woken by closest neighbors who are awake or by closely related individuals even when they are not closest neighbors or by a minimum proportion of awake individuals in the group) and when (different delays in waking up once the awakening criterion has been met might lead to different collective patterns). Coupling collective sleep models with individuals' sensory fields [50] (Figure 2F) provides the opportunity to formulate testable hypotheses about collective responses to external stimuli [e.g., detecting an approaching predator (thereby enhancing survival) or triggering 'false alarms' [51] (thereby leading to loss in sleep duration and increase in sleep fragmentation)] and quantify their fitness outcomes [52].

Analyzing social sleep

Broadly speaking, social sleep can be analyzed in terms of spatial arrangement and temporal sleep patterns. The spatial arrangement of individuals relative to others during the sleeping period can be characterized by a 'sleep proximity network', similar to proximity networks that are computed from data collected during the waking period. Temporal sleep patterns can be characterized by a time series we term 'iSleep' that describes the temporal progression of sleep states in an individual, obtained by scoring sleep measurement data (see Box 1 for details on sleep measurement techniques). Scoring is done either based on domain knowledge by an expert, or through automated classification [53]. Depending on the measurement approach, iSleep will describe the duration and timing of transitions between different numbers of discrete sleep states (Figure 1, right panel), for example, two {awake, asleep} (e.g., Figure 2A), three {awake, REM sleep, non-REM sleep}, etc. Metrics such as sleep timing, duration, and fragmentation can be computed from iSleep and compared with social and group traits. Synchronization between the iSleeps of two individuals can be quantified based on normalized root mean squared difference in sleep states over a given time interval (e.g., 24 h; metric described in Figure 2C). Information on degree of synchronization between iSleeps for all pairs of individuals can be combined in a 'sleep synchronization network' (Figure 2C).

Information on differences in the timing of sleep onset and awakening between pairs of individuals [32] can similarly be combined in 'sleep timing networks' (one network to



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Figure 2. Analysis of social sleep. (A) A toy example showing 24-h (noon to noon) sleep-state time series (iSleeps, with 'asleep' encoded by the number 0 and 'awake' encoded by the number 1) of a meerkat (*Suricata suricatta*) group of six individuals, U–Z. U, V, and X slept uninterrupted throughout the night but went to sleep and/or woke up at different times. W slept later and woke more frequently than the others. Y, a female, woke up during the night at the same time as male Z's second nighttime awakening, perhaps to copulate with Z. (B) gSleep, a time series describing the aggregate sleep state of the entire group, calculated here as the proportion of individuals in the group that were asleep at each time point. (C) The degree of sleep synchronization between two individuals (U and V) can be quantified by applying the proposed metric to their iSleeps $u[t]$ and $v[t]$. t indicates time, L indicates the length of time over which synchronization is computed (here, 24 h, but can otherwise be shorter depending on the research question), M indicates the numeric code assigned to the 'awake' state (here, 1), and m indicates the numeric code assigned to the 'asleep' state (here, 0) or the deepest sleep state if sleep heterogeneity was recorded. The proposed metric is designed to yield a value between 0 and 1 regardless of the precise choice of M and m , and to ensure that in the particular (hypothetical) case where the iSleeps of both individuals are identical and encoded as 0 throughout the period L , the degree of synchronization is maximal (i.e., equal to 1), as should be the case for any pair of identical iSleeps (a correlation-based metric would have yielded a synchronization of 0 in this particular case, thereby incorrectly implying that the identical iSleeps were not synchronized). Synchronization values computed for all pairs of individuals can be used to construct an adjacency matrix that can be visualized as an undirected weighted 'sleep synchronization network'. The adjacency matrix and network shown here were computed from the iSleeps in (A). (D) Differences in the timing of awakening (and sleep onset, not shown here) can similarly be represented as a directed weighted 'sleep timing network' [shown here with its adjacency matrix (entries in minutes)]. (E) Collective sleep models inspired from the field of collective behavior can be used to explore aggregate group-level sleep behaviors such as the 'wave of wakefulness' propagating through the group shown (gray: asleep; orange: awake). (F) Coupling collective sleep models with individuals' sensory fields can help to explore collective responses to external stimuli during the sleeping period. Illustration of meerkat faces by Javier Lázaro.

summarize information on sleep onset and another for information on awakening; Figure 2D). Such networks would be characterized by adjacency matrices with positive values (in units of time, for example, minutes) when the column individual's sleep onset (awakening) lags the row individual's sleep onset (awakening) and zeros when the delay is negative or zero (e.g., on the diagonal, where individuals will have zero delay compared with their own sleep onset/awakening; Figure 2D). Sleep synchronization and sleep timing networks can be used to

investigate how individuals copy, lead, and follow the sleep–wake behavior of others in the group and model the collective dynamics that emerge. Analyzing sleep networks using existing tools from animal social network analysis [54] will help to reveal and study emergent sleep processes at the group level. For example, network metrics can help capture the expected importance of specific individuals in driving the sleep states of others or the overall connectedness and degree of clustering present in sleep networks. Moreover, exploring connections between individuals' positions in sleep networks and their long-term survival and fitness can help to reveal the adaptive value of social sleep from an evolutionary perspective.

The collective dynamics of sleep can be studied using a time series that describes the sleep state of the entire group. The group sleep time series, which we term 'gSleep', can be obtained by pooling together the iSleeps of all individuals in the group by calculating the proportion of individuals that are asleep at a given time [48,55] (Figure 2B) or computing other measures such as the mode, median, or mean of iSleep values across individuals for every time step. Spectral analysis of gSleep (e.g., using periodograms) can unravel group-level sleep patterns. gSleep may be periodic, where a large proportion of individuals in the group sleep and awaken synchronously and at regular intervals [48], or synchronous but aperiodic, where individuals sleep and awaken together but not at regular intervals. The absence of clear patterns in gSleep may indicate asynchronous sleeping patterns [34], which can be further investigated by pooling the iSleeps of subgroups of individuals and then comparing the pooled time series for the different subgroups. Sleep in multiple neighboring groups can be analyzed by treating gSleep in a multi-group setting analogously to iSleep in a multi-individual group. These methods can also be extended to polyphasic sleep (where multiple short sleep bouts occur over a 24-h period) by applying them to shorter blocks of time (e.g., 30 min to a few hours instead of 24 h) and to unihemispheric sleep by considering multistate iSleeps (e.g., {awake; unihemispheric sleep; REM sleep; non-REM sleep in both hemispheres of the brain simultaneously}). Ultimately, by analyzing sleep at individual (iSleep), dyadic (sleep networks), and group (gSleep) scales, we can begin to quantify the variation in sleep patterns observed across levels of social organization, allowing us to link these levels to one another and to their ecological and evolutionary drivers.

Measuring sleep in social animals

Understanding the interplay between sociality and sleep requires measuring sleep while it occurs within its natural social context (Box 1 and Figure 1). While electrophysiology allows fine-grained identification of sleep stages, these methods are challenging to implement outside the lab or scale to large numbers of interacting individuals. Behavior, on the other hand, can often be used to quantify sleep across a variety of contexts and species (Table 1 and Box 1), creating an opportunity to bridge the domains of animal behavior and sleep science. The most common behavioral indicators of sleep include motionlessness, stereotypical body postures, closed eyes, and reduced muscle tone (exceptions reviewed in [5,6]), with prolonged inactivity being strongly predictive of elevated arousal thresholds in some species [6]. In addition, behaviors associated with transitions between sleeping and waking can be used to understand the social regulation of sleep; yawning, for example, is pervasive across vertebrates, is associated with sleep onset and offset, and is socially contagious [56]. While validation of behavioral proxies of sleep against electrophysiological measurements remains crucial (see Box 1 for further commentary), these similarities in how sleep is expressed (Table 1) promise to facilitate the study of social sleep since behavioral proxies are generally easier to measure, cheaper, less invasive, and better suited for simultaneous monitoring of groups of individuals, particularly in field conditions.

Box 1. Studying sleep in the wild

A diverse methodological toolkit now exists for studying sleep in natural settings (reviewed in [5,6]). Broadly speaking, three main types of data contribute to our understanding of sleep behavior: (i) 'electro' [electrical signals recorded from the animal's body that quantify brain activity (electroencephalography; EEG), muscle tone (electromyography), and eye movement (electrooculography)], (ii) 'stimulo' [experimental stimulation (e.g., mechanical and acoustic) to gauge arousal threshold], and (iii) 'behavioral' [behavioral observations (e.g., movement, posture, and eye closure)]. When used together (we term this the 'electro–stimulo–behavioral' approach; see Table 1), these three datastreams provide a baseline description of sleep detection, depth, and heterogeneity, a particularly important step when sleep is being investigated for the first time in a particular study species or taxonomic group. Sleep detection is the ability to distinguish sleep from waking. Sleep depth refers to the extent of reduction in responsiveness to external stimuli and is thought to be a correlate of the intensity of ongoing sleep processes. Sleep heterogeneity refers to the variation in electrical activity (of the brain, muscles, and/or eye), behavior, physiology, and/or sleep depth during sleep [3], sometimes manifesting as discrete states (e.g., REM and non-REM sleep). Electro–stimulo–behavioral methodology can be used to develop reliable proxies for sleep detection and possibly also for sleep depth and heterogeneity, based on behavioral data alone. For example, a recent study on northern elephant seals (*Mirounga angustirostris*) used EEG, heart rate, and behavioral measurements to develop a sleep detection model based on behavior alone; application of this model to data collected in wild seals revealed differences in sleep cycle duration as a function of dive depth [7]. Behavioral proxies of sleep can, in some cases, also quantify sleep heterogeneity; for example, some cephalopods (octopus, *Octopus laqueus*) exhibit clear behavioral signs of two distinct sleep states associated with elevated arousal thresholds and changes in brain activity [60]. However, behavioral proxies can confound quiet wakefulness with sleep [61] and fail to detect unihemispheric sleep [61] or reduction in sleep need achieved through other means, such as during rumination by reindeer (*Rangifer tarandus tarandus*) [62]. Best practice is to validate behavioral sleep proxies against electrophysiological measurements and characterize the accuracy of behavioral sleep quantification. While advances in instrumentation technology should eventually make electrophysiological validation of sleep in the wild less invasive and more logistically feasible, insistence on electro–stimulo–behavioral methodology will stymie social sleep research. While some questions will lend themselves to 'sleep-first' approaches, wherein study taxa can be chosen based on ease of sleep validation, many questions will require 'species-first' approaches owing to taxonomic considerations inherent in comparative research or the need for longitudinal information on individual life histories and social structure. Such information is often available only at established long-term study sites, where invasive measurement could cause loss of animal habituation and consequent disruption of research on-site. For such studies, use of alternative terminology when reporting behavioral sleep measures (e.g., 'sleep-like state', 'behavioral sleep', 'inactivity', and 'resting'; see Table 1) might offer a reasonable way forward.

Table 1. Sleep measurement^a

Methodological approach		Detection	Depth	Heterogeneity
Electro-stimulo-behavioral		✓	✓	✓
Electro-behavioral		✓	✓	✓
Stimulo-behavioral		✓	✓	?
Behavioral only	Observation	✓	?	?
	Motion sensing	✓	?	?
	Indirect signs	✓	×	×

^aApproaches to measure sleep fall on a spectrum. The most comprehensive electro–stimulo–behavioral approach [63] lies at one end, intermediate approaches such as electro–behavioral (parallel measurement of electrophysiology and behavior but no explicit measurement of arousal threshold [22]) and stimulo–behavioral (parallel measurement of arousal threshold and behavior [64]) lie in the middle, while behavioral-only approaches (Table 1) lie at the other end. Behavioral-only approaches can vary from visual observation [65] to sleep inference from animal-borne motion sensors [20] to indirect observation of signs of waking (e.g., animals coming out of their sleeping burrow after the sleeping period) [18]. Green boxes indicate that the aspect of sleep (detection, depth, or heterogeneity) can be reliably measured with the method. Yellow boxes indicate that measurement or inference is possible but likely not with the same accuracy or reliability as with the electro–stimulo–behavioral approach [66,67]. Red boxes indicate that measurement or inference is not possible. White boxes with question marks indicate that measurement or inference is not yet known.

Table 1. Behavioral sleep quantification and applications^a

Type of sleep measurement	Behavior	Measurement method	Species	Sleep quantification	Insights gained	Validation of sleep proxies	Refs
Detection	Inactivity	Accelerometry	African elephant (<i>Loxodonta africana</i>)	Inactivity for at least 5 min, measured by subcutaneously implanted actiwatch in the trunk. In addition, a recumbent sleeping position, during which REM sleep likely occurred, was derived from accelerometer readings.	Nocturnal, polyphasic, 2-h sleep in elephants, with frequent use of new sleep sites.	Authors indicated that they used the term 'sleep' to mean 'inactivity'. They stated that the anatomy of the elephant skull would make surgery to implant EEG electrodes highly invasive.	[70]
			Javan slow loris (<i>Nycticebus javanicus</i>)	Actigraphy scores (activity counts at 1-min epochs) were used to devise criteria for behavioral sleep/rest. Inactivity was defined as an activity score of zero over a 1-min epoch. Interruptions in rest lasting 5 min or less were classified as 'brief awakenings'.	Illumination and ambient temperature had a major influence in shaping 24-h patterns of activity and rest.	Actigraphy-derived immobility was termed 'sleep' based on a previous validation of actigraphy against EEG in marmosets (<i>Callithrix jacchus</i>).	[71]
			Olive baboon (<i>Papio anubis</i>)	Sleep was identified using an algorithm based on dynamic body acceleration values remaining below a threshold for at least 3 min.	Sleep duration decreased at less familiar sleep sites and when sleeping in proximity to more individuals. Individuals had synchronized patterns of waking during the night. No evidence for compensation for lost sleep.	The body acceleration-based sleep detection algorithm was adapted from human studies that have been extensively validated against polysomnography. In addition, the baboon sleep detection algorithm was validated using observations of postural change made with thermal imagery. Natural experiments arising from the awakening and movement of neighboring group-mates were used to assess changes in arousal threshold.	[20]
	Body posture	Video, accelerometry	Sperm whale (<i>Physeter macrocephalus</i>)	Shallow 'drift-dives', which occur in stereotypical vertical postures just below the sea surface, were detected using speed and accelerometer-derived pitch angle.	Sperm whales rest by drifting vertically under the sea surface.	Authors used the term 'rest' instead of 'sleep'. Whales were observed to be nonresponsive to closely passing vessels until these inadvertently touched them, which suggested elevated arousal thresholds during these resting dives.	[72]

(continued on next page)

Table 1. (continued)

Type of sleep measurement	Behavior	Measurement method	Species	Sleep quantification	Insights gained	Validation of sleep proxies	Refs
	Inactivity, body posture	Video	Great tit (<i>Parus major</i>)	Sleep was characterized by inactivity and a stereotypical sleep posture (feathers fluffed and beak tucked back into the scapular feathers) maintained for at least 30 s. Awakenings during the night were identified using motion detection software.	Within-individual plasticity in sleep behaviors. Sleep was related to season, sex, age, and the environment. Individuals in captivity went to sleep later and slept less than those in the wild.	Authors used the term 'behavioral sleep' and cautioned that purely behavioral definitions of sleep could confound quiet wakefulness and sleep and would be unable to detect unihemispheric sleep.	[61]
		Drone imagery	Feral horse (<i>Equus ferus</i>)	Photographs were taken from 30 to 50 m above the ground using drone-mounted cameras at 30-min intervals from 09.00 h to 18.00 h. Horses were said to be resting if they did not move from one image to the next and held stereotypical resting postures (lying down or standing still with their neck parallel to the ground).	Feral horses living in a multilevel society synchronize their activity-inactivity patterns within and between their primary social units. Synchronization within units is stronger than that between units in the herd.	Authors did not use the term 'sleep' to describe the behavior they detected, instead using the term 'resting' throughout.	[73]
	Inactivity, body posture, eye closure	Direct observation	Gulls (<i>Larus</i> spp.)	Inactivity in a stereotypical posture (standing on one leg or crouched or bill tucked under scapulars) with eyes closed was used to identify sleep.	Copying of neighbor vigilance in sleeping groups. Collective waves of sleep in groups.	The study's main focus was to monitor vigilance, and 'sleep' was viewed as a 'low vigilance state'.	[45,48]
	Head-muscle tone, face/limb twitching, eye closure	Video	Orangutan (<i>Pongo</i> spp.), Guinea baboon (<i>Papio papio</i>)	One-minute epochs in videos were manually scored as 'wake' or 'sleep'. Sleep was defined by closed eyes with no movement, reduced muscular tone, and face/limb twitching.	Captive orangutans experienced deeper, more efficient sleep than captive baboons.	Authors argued that polysomnography was invasive and impractical for primate sleep research. The proxies used for 'sleep depth' were motor activity during sleep and sleep fragmentation (the use of these metrics was justified based on their correlation with previously validated measures of sleep depth in humans and nonhuman primates).	[65]

Table 1. (continued)

Type of sleep measurement	Behavior	Measurement method	Species	Sleep quantification	Insights gained	Validation of sleep proxies	Refs
Heterogeneity	Sleep stage-specific body posture	Video	Angolan giraffe (<i>G. giraffa angolensis</i>)	Behavior classified into active, resting (based on lying posture), and REM sleep. Resting classification was based on lying posture. REM sleep classification was based on specific postures linked to REM sleep in a previously published study, sustained for more than 10 s.	Activity patterns linked to photoperiod and season. REM sleep posture only observed after sunset. All individuals in a group never slept simultaneously (while some slept, others were awake and vigilant). Sleeping site changed nightly.	Justification for REM sleep identification was the observation of short, spontaneous movements of the ears, eyes, or neck while giraffes adopted the characteristic posture linked to REM sleep.	[34]
	Eye and limb movement	Infrared videography	Jumping spider (<i>Evarcha arcuata</i> , Salticidae)	Retinal movement, leg-curling, stretching, and cleaning behavior were manually scored in videos. REM sleep-like behavior was characterized by retinal movements accompanied by leg-curling or twitching limbs. A neural network was trained to estimate the angular movement of retinas.	Identification of REM sleep-like behavioral state.	Authors used the term 'REM sleep-like' instead of 'REM sleep.'	[74]

^aA nonexhaustive list of studies using different datastreams to capture behavior for quantifying sleep in a range of animal species, along with insights on individual, comparative, and social sleep. Generally speaking, field studies of animal sleep eschew electrophysiological and arousal-threshold measurements that are aimed at validating behavioral proxies for sleep since these are often invasive and/or impractical. Consequently, it is currently not common for such studies to conduct stringent validations of behavioral criteria used to define sleep; they often use alternative terminology such as 'inactivity', 'resting', 'behavioral sleep', or 'sleep-like state' to describe the behavioral state that they measure.

Inactivity can be measured in several ways, such as via direct or video-based observation or motion sensors attached to the animal (e.g., accelerometers [20,57]). Both methodologies usually require an additional step where manual annotation or algorithms are used to identify behavioral sleep. Although the details necessarily vary from species to species (see Table 1), identifying 'prolonged inactivity' essentially requires two ingredients: a motion/behavioral threshold to separate inactivity from activity and a duration range to classify a bout of inactivity as behavioral sleep (with a lower bound that is long enough to reject brief pauses between successive active bouts and an upper bound that is short enough to separate sleep from torpor, hibernation, and death). Behavioral sleep detection alone can lend valuable insights into changes in sleep duration, timing, and fragmentation associated with social interactions during the sleeping period. Whether behavioral observations can also be used to quantify sleep depth and heterogeneity and how electrophysiology can be better adapted to measuring social sleep are open questions (Box 1 and see Outstanding questions). Sleep substates like REM and non-REM sleep are difficult to assess using behavioral proxies, and electrophysiology is still often mandatory to precisely detect and quantify these states. Finally, thermal imaging is a physiological measure that could be used to track sleep in homeothermic animals. Core body temperature rapidly declines following sleep onset and remains low throughout the sleeping period [58]. These changes could potentially be detected using thermography.

Concluding remarks

Social sleep is a research frontier that we believe holds exciting potential for new insights into both sleep science and wild animals' lives. We argue that interactions during the sleep period contribute in important, but largely overlooked, ways to group social dynamics, while patterns of social interaction, group decision-making, and the structure of social connections within animal groups play important, but poorly understood, roles in shaping sleep behavior. Interesting questions abound at the individual, dyadic, and group levels, and capitalizing on these opportunities will likely require methodological innovations to overcome the logistical difficulties of measuring sleep and sociality in multiple animals simultaneously over meaningfully long periods of time (see section 'Research at the interface of sleep and sociality' and Outstanding questions). The application of validated behavioral criteria for sleep quantification (see Box 1) in group-living animals studied at long-term field sites can be an effective launchpad for systematic investigation of social sleep. Such long-term studies often have a wealth of past and current social and ecological data, including individual life histories, dominance hierarchies, kin and affiliative relationships, spatial and temporal variability in resources, weather conditions, etc., that can provide the necessary context for nuanced analyses of social sleep. We point to the importance of empirical studies spanning both the waking and sleeping periods [such data can often be tremendously informative even for studies that are not directly related to questions of social sleep (e.g., [59])] on multiple groups of the same or similar species and comparing across species (see Outstanding questions). By collecting data on sleep and sociality and applying our proposed tools to analyze social sleep, we can begin unraveling the adaptive functions and evolutionary trade-offs of sleep that may not be revealed by studying individual animals alone.

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Declaration of interests

The authors declare no competing interests.

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Outstanding questions

What are the eco-evolutionary causes and consequences of animals sleeping in groups?

Are the costs and benefits of sleeping in groups distributed equally across individuals in the group?

How does social sleep differ across group-living vertebrates and invertebrates, and why do these differences arise?

How does social structure (e.g., dominance hierarchy, social centrality, and affiliative and kin relationships) influence individual sleep?

How do group traits (e.g., size, demographic composition, and degree of cohesion) influence individual sleep?

In group-living species, are individuals' sleep states coupled? And does this lead to the propagation of sleep states through the group and the emergence of collective dynamics of social sleep?

How do social interactions during the sleeping period differ from, influence, and get influenced by social interactions during the waking period?

How does sleep quality affect social interactions during the waking period? Poor or insufficient sleep can, for instance, affect how effectively and accurately animals communicate with each other, which will have knock-on effects for the whole group's behavior.

Do social sleepers sleep differently from solitary sleepers? Reduced sleep may be the price that social sleepers pay to lower predation risk during the sleeping period through dilution and multiple potential sentinels.

How can behavioral approaches to sleep measurement be expanded and/or adapted to reliably quantify sleep depth and heterogeneity?

How can electrophysiological approaches and tools to measure sleep be expanded to invertebrates and adapted to facilitate the measurement of social sleep in the wild?

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