Title
The Physiology, Behavioral Ecology, and Collective Dynamics of Sleep in Wild Olive Baboons (Papio anubis)

Author
Loftus, J. Carter

Publication Date
2022

Peer reviewed|Thesis/dissertation

The Physiology, Behavioral Ecology, and Collective Dynamics of Sleep in Wild Olive Baboons (*Papio anubis*)

By

J. CARTER LOFTUS

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Animal Behavior

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Margaret Crofoot, Co-Chair

Damien Caillaud, Co-Chair

Lynne Isbell

Andrew Sih

Committee in Charge

2022

Table of Contents

Acknowledgements

The phrase “it takes a village” could not be more applicable than when describing a dissertation. I could not have even begun this dissertation without the support of many family members, friends, and mentors. So, I will start with a broad “thank you” to all of the people that have guided my development as a scientist and as a person, contributed to my intellectual growth, helped me overcome challenges, cared for me during trying times, celebrated with me after exciting accomplishments, or even just distracted me when I needed a good distraction. Naming you all could fill this entire dissertation.

First and foremost, I would like to thank my primary supervisors and research mentors: Meg Crofoot and Roi Harel. Meg, you are truly a visionary, and your vision has pushed me to take on challenges that I never would have approached without you. You have made me not only a better scientist, but a stronger, more capable, and more confident person. Thanks to you, I am completing my dissertation proud of the work that I have accomplished and the person that I have become. I will always have you to thank for the opportunities that lie ahead of me. Roi, you have been an all-in-one friend, mentor, supervisor, support system, and grounding force during some of the most stressful but also rewarding times of my life. Whether it was staying up all night with me collecting data in Kenya, calming me down when I was stressed about a deadline, or even just having me over for dinner with your family, you have been there for me at every step of this Ph.D., and I don’t think I could have done it without you. Meg and Roi, I will miss working with you both tremendously.

I would like to thank my dissertation committee: Meg Crofoot, Damien Caillaud, Andy Sih, and Lynne Isbell. Damien, thank you for all of your guidance throughout my Ph.D., but also for taking me on as your own student in this final stretch, so that I could complete my dissertation in Germany with relatively minor administrative hurdles. Andy, thank you for helping me get started with this graduate school journey, and providing research ideas and inspirations that have continued to have a formative influence on my work throughout my dissertation research. Thank you also for your affinity for throwing great karaoke parties. Lynne, thank you for your generosity as a mentor and

collaborator, and your willingness to always contribute your time and knowledge in helping me form my project ideas. I have always had a great time working with you.

I want to thank the PIs and post-docs that have provided critical research mentorship and training during both my graduate and undergraduate years: Meg Crofoot, Damien Caillaud, Andy Sih, Lynne Isbell, Ari Strandburg-Peshkin, Tom Hahn, Tom Seeley, Roi Harel, Chase Núñez, Shauhin Alavi, and Michael Smith. This dissertation would not be what it is, nor would I be the scientist I am, without your investment in me, my research, and my future.

Thank you to our baboon research team, Alison Govearts, Chase Núñez, and Roi Harel. Over the last few years, you have contributed to everything from the formation of major data collection plans to single word choice discussions in the tenth revision of an abstract, and I have appreciated it all!

I would like to thank the many collaborators who made this dissertation possible. Thank you to: Sonja Wild for helping with many major aspects of this final push to the end of the Ph.D., but most notably, the network-based diffusion analysis; Ben Koger for providing the code, time, and advice that has made the automated tracking of baboons in infrared imagery possible; Alie Ashbury for dealing with my panicked state while guiding me through—sometimes sentence by sentence—almost all of the writing I have done since (literally) the day you started working here (and for the comic relief that you have provided along the way); Shauhin Alavi for all of the statistical advice you have provided, but, most importantly, for your unbelievable response time to my several "statistical emergency" Slack messages that I have sent between the hours of midnight and 5:00 AM; Rasmus and Linnea Havmøller for thinking of exciting research ideas worth pursuing together and for knowing when it's time for me to take a break from the work and have some fun; Akiko Matsumoto-Oda for allowing me to work with the group of baboons that she habituated and for providing critical expert-knowledge during our collaboration that made my project possible; and to Adrian Perez for being a great friend, and for continuing to be a fun, upbeat, and compassionate collaborator, even after our project continued for a few more years than either of us had planned. I have had a wonderful experience working with you.

To all of the people who helped me annotate training data for machine-learning algorithms or manually correct the tracks in the infrared imagery: Edward De Kock, Vilson Karaj, Zsófi Szegleti, Victor Tan, Dario Walser, Jana Kirsch, Arianna Flood, Christian Menne, Elizabeth Neuhaus, Anushka Vispute, Ryan Bauer, Denise Ilogu, and Thomas Maisch. I truly could not have done it without you!

Thank you to our baboon field team. Andrea, Lepaip, and Zakayo, you are the unsung heroes of all the work that we produce. You have all independently saved me from being trampled by a buffalo on multiple occasions, so it is quite literally true when I say that I wouldn't be here without you. Your knowledge of baboons and their ecosystem, more broadly, has also been essential in shaping my research.

I would like to thank the Animal Behavior Graduate Group at UC Davis, the Max Planck Institute of Animal Behavior, and Mpala Research Centre, both for the administrative support they have offered, but also for the communities of friends that they provided me during my Ph.D. I have had a fantastic time with you all.

To my original lab-mates that started this journey with me: Grace Davis, Claudio Monteza, Alexander Vining, Roi Harel, and Shauhin Alavi. We have been around the world together, and it's been a wild ride. I will miss you greatly. (And a special thank you to Grace Davis for teaching me much of what I know about baboons!)

Thank you to the career counselors that helped me find my way beyond graduate school, Tory Wobber, Candace Crowley, and Sumiko Hong. You solved a lot of existential crises!

I would like to thank the sources that funded my research and my stipends throughout my graduate school career: a National Science Foundation Graduate Research Fellowship, the National Science Foundation Graduate Research Internship Program, a National Science Foundation Doctoral Dissertation Research Improvement Grant, a Dean's Distinguished Graduate Fellowship from the University of California, Davis, the Richard G. Coss Wildlife Research Fellowship, and an Achievement Rewards for College Scientists Fellowship.

I want to thank the many friends that supported me along the way, with a special shout-out to Tim Hermann and Matthew Clardy. Tim, whether with working out or with drinking a beer on the bridge (because it was the only place we were legally allowed to drink a beer together), you kept me

sane during lockdown (and beyond!). To Clardy, my biggest cheerleader: the pangs of loneliness that can sometimes set in when living in a foreign country were never a problem when you were just a phone call away. Thanks for always having my back. I can't wait to see what New York City has in store for us.

Last, but most certainly not least, I would like to thank my family: my parents, Jon and Tayloe Loftus; my brother, David Loftus, and his girlfriend and my future business partner, Ali Verbeck; my sister, Elizabeth Loftus-Reich; my brother-in-law, Paul Reich; and my aunt and godmother, Amy Kimm. You guys have truly been there for it all. You've revised a million applications, manuscripts, and grant proposals. You've proofread my resume and practiced interviews with me. You've travelled with me in my new state, and then in my new country. You've made me feel at home in Germany. You've invited me to live with you during the most isolating times of the pandemic (and never missed a weekly dance party while I was there). You've reminded me that life can happen along the way to getting a Ph.D.: celebrating weddings and new family members-to-be, playing pitch in the middle of the night, karaoke-rap-battling our way through holidays, and skiing in the Alps. You've carried me through the sometimes debilitatingly challenging parts of this Ph.D., but, more importantly, you've celebrated with me all the accomplishments—big and small—along the way with a bottle of champagne and a good time always at the ready. I don't know if I could have done it without you, but I know that I wouldn't have wanted to try. I am looking forward to our next adventure together.

Dedication

I would like to dedicate this dissertation to my mother, Tayloe Loftus. Before she was diagnosed with Early-Onset Alzheimer's Dementia at the young age of 55, my mother was a brilliant and passionate physician, who cared deeply for her patients with a level of empathy that was impressive even to my indignant teenage self. But—aside from being a mother and wife—she was, first and foremost, an educator and mentor. Having taught medical school for almost 20 years and serving as the president of the national organization of medical school clerkship directors, she had her primary influence on patients through the formation of their future doctors. I have had the pleasure of getting to see some of her former students carry forward her characteristic blend of extreme intelligence and sincere compassion. My mother has demonstrated to me that while the knowledge we gather for ourselves is exceedingly fragile, the knowledge that we share with others will live forever. And so, without further ado, here is the knowledge that is mine to share.

Abstract

All animals, from honeybees to humans, devote a portion of their daily lives to the quickly reversible state of diminished responsiveness to external stimuli known as sleep. The ubiquity of sleep across taxa reflects its importance. Sleep plays a vital role in supporting critical physiological processes by maintaining the central nervous system, supporting the immune system, and enhancing cognition. Accordingly, periods of insufficient investment in sleep can lead to severe health consequences. However, this state of reduced awareness leaves animals highly vulnerable to their predators, and presents substantial opportunity costs by precluding animals from engaging in the many other activities that are also essential to their fitness. Individuals thus navigate a series of trade-offs in making decisions about investing in sleep. In groups of social animals, individuals' choices about when, where, and how to sleep may be further affected by the behavior of nearby conspecifics, both within, as well as outside of, their group. However, to date, most sleep research has relied on polysomnography—an exceptionally thorough, yet relatively invasive technique for measuring sleep—which has largely confined sleep research to the laboratory. This constraint obscures our understanding of how ecologically and socially relevant contexts both shape and are shaped by sleep dynamics. The established research paradigm has therefore perpetuated a substantial gap in our knowledge of one of the most universal behaviors in the animal kingdom.

My dissertation makes a critical step towards filling this gap by introducing novel methods to bring sleep research into the wild, and implementing these methods to shine important light on the interdependencies between an animal's behavioral ecology and its sleep physiology. In the course of my research, I asked and answered fundamental questions about how sleep manifests in the wild at three scales of biological organization: the individual, the group, and the population. To address these questions, I leveraged collar-mounted accelerometers to monitor the sleep patterns of wild olive baboons (*Papio anubis*) and validated the accelerometer-based sleep classification against high-resolution infrared videography. The chapters of this dissertation focus, respectively, on the individual, group, and population scales, each using a distinct dataset of GPS locations and accelerometry collected from the baboons that range near Mpala Research Centre in Laikipia, Kenya.

These baboons' nocturnal vulnerabilities and well-studied social dynamics, both within and between groups, make them an ideal system for studying reciprocal connections between the ecological and social environment and sleep behavior.

Chapter 1 investigates how individuals balance their physiological sleep imperative with the ecological and social pressures that render sleep costly in the wild. By analyzing the sleep duration and intensity of 26 members of a group of wild baboons, I compared the influences of homeostatic regulation, the physical location in which individuals slept, and the local social environment during the sleep period on baboon sleep behavior. I found that, in stark contrast to findings from studies in the laboratory, the recent history of sleep and activity (i.e. factors pertinent to homeostatic regulation) played a relatively minor role in shaping the sleep patterns of wild baboons. Ecological and social pressures, on the other hand, had a substantial influence on sleep. Namely, baboons slept less when sleeping in unfamiliar environments and when sleeping in proximity to more group-mates, and they did not appear to compensate for this sleep loss with higher intensity sleep. These results suggest that sacrificing sleep when in risky habitats and to interact with group-mates during the night might be adaptive for animals whose fitness depends critically on avoiding predation and maintaining strong social bonds. Beyond its immediate research findings, this chapter establishes the validity of a new method for measuring the sleep of wild animals, which I also implemented in the research described in the subsequent dissertation chapters. Furthermore, it opens an exciting new frontier of scientific exploration into the social dynamics of sleep by demonstrating a collective signature of sleep in gregarious animals.

Chapter 2 builds upon the findings of Chapter 1 with a venture into this new frontier, investigating the mechanisms and consequences of collective sleep dynamics. To shed light on how variation among group-mates and the relationships they share with each other influenced their sleep patterns, I returned to Mpala Research Centre to measure the sleep patterns of 26 members of a different group of wild baboons. I supplemented these sleep data with a complete account of the nighttime positions and movements of group members that I extracted from infrared video using computer-vision tracking of the baboons in their sleep site. Using information-theoretic and network-based diffusion analyses, I found that synchronized periods of waking during the night resulted from

social disturbances of sleep that propagated primarily through the group's affiliative network and, to a lesser extent, its dominance network. Analysis of the nocturnal movements of group members indicated that spatial proximity to an awakening group-mate during the night was not sufficient to cause an individual to become active. Thus, the spatial network was not solely responsible for guiding the propagation of wakefulness during the night, but rather the affiliative and dominance networks, independent of the spatial network, also contributed to shaping collective waking dynamics. Asymmetries in the influence that individuals have over their group-mates' sleep patterns led socially central individuals to sleep less than their socially peripheral counterparts. These results demonstrate that the collective dynamics in a highly structured animal society create costs to sleep investment that are disproportionately borne by socially central individuals. However, this sleep loss may represent an adaptive sleep sacrifice that provides socially central individuals with more opportunities to maintain the social bonds that are essential to their higher fitness.

Chapter 3 scales the study of the social dynamics of sleep to the population level, and explores, for the first time, bi-directional feedbacks between the social environment and sleep dynamics. I analyzed the movements and sleep patterns of select members of four neighboring baboon groups to understand how encounters between distinct social groups influence sleep, as well as how sleep dynamics, in turn, influence the relationships between neighboring groups. I discovered that sharing a sleep refuge with a neighboring group impaired sleep quality. Specifically, baboons experienced shorter duration, lower efficiency, and more fragmented sleep when sharing a refuge with another group compared to when sleeping as lone groups. However, sleeping together catalyzed tolerant interactions between groups that continued well beyond the sleep period. Groups were more likely to interact and these interactions were more likely to involve extended, cohesive movements after spending the night at the same site than after sleeping at separate sites. A movement path randomization analysis confirmed that these tolerant interactions deviated from the interactions expected by chance, and revealed that they scaled up to define broader relationships of tolerance between study groups across the study period. These results suggest that sacrificing sleep in a shared sleep refuge, potentially in favor of engaging in social interactions with members of the other group

sharing the refuge, may play an important role in establishing relationships between groups and, thus, shaping the social organization of a population.

Taken together, these chapters demonstrate that selectively sacrificing the vital benefits of sleep—when in risky environments, and when there may be opportunities to develop and maintain social bonds, not only with group-mates but also with individuals from other social groups—may represent key adaptations in the wild. These sleep sacrifices may have important implications not only for the fitness of an individual but also for the collective dynamics of a social group and even the social organization of an entire population. By revealing the importance of social and ecological pressures—pressures that are absent in laboratory settings—in shaping sleep behavior, my dissertation research highlights the importance of studying sleep in the wild, where the adaptive value of sleep directly reflects the complex trade-offs that have guided its evolution. This dissertation also paves the way for a new body of research that explores the fitness consequences of the strategies with which individuals navigate the sleep trade-offs demonstrated by this research. Such exploration has the potential to shed critical light on one of biology's greatest mysteries: the evolution of sleep.

Introduction

As humans, we spend approximately one-third of our lives asleep, in a rapidly reversible behavioral state characterized by reduced responsiveness to our surroundings (Nunn et al., 2016). Sleep shapes the world in which we live: it structures our days (Takahashi, 2012), influences our productivity (Rosekind et al., 2010), and molds our perspectives (Ben Simon et al., 2020). Sleep exerts further influences in ways that may be subtler to us as we go about our daily lives, playing an essential role in the efficient functioning of almost all physiological processes (Zielinski et al., 2016). Most notably, sleep is critical to the development and maintenance of our central nervous system, the support of our immune response, the advancement of our cognition, and physical repair of our cells (Zielinski et al., 2016). Given the time that we devote to it and the many functions it performs, it is perhaps unsurprising that sleep is not a voluntary behavior, but rather a physiological imperative, with extended periods of sleep deprivation leading to an in increased risk of obesity, hypertension, heart disease and immune system dysfunction (Almeida & Malheiro, 2016; Gangwisch, 2014; Knutson et al., 2007; Mullington et al., 2009; Taheri, 2006). Despite the importance of sleep and the health consequences of insufficient investment in sleep, one in three Americans is sleep deprived (Sheehan et al., 2019). Although sleep deprivation can result from a number of medical disorders, a primary cause of sleep deprivation is actually the intentional sacrifice of sleep in favor of commitments that require our waking attention (Murphy & Delanty, 2007). These sleep sacrifices can even bring about increased measures of success (Kasaeian et al., 2019), highlighting the trade-offs that we face when deciding how to invest our finite time.

Our need for sleep and the trade-offs that accompany it are not unique. Every animal studied to date devotes a portion of each day to a period of diminished responsiveness to external stimuli (Cirelli & Tononi, 2008). Many laboratory studies have confirmed that, as in humans, sleep is essential to health and survival in animals, with potentially fatal repercussions of extreme sleep deprivation (Luyster et al., 2012; Mahowald & Schenck, 2005; Rechtschaffen & Bergmann, 2002). The importance of sleep to the fitness of non-human animals (henceforth, animals) and humans alike is emphasized by its homeostatic regulation—following periods of sleep deprivation, individuals

experience subsequent sleep bouts that are particularly long and intense (Kitamura et al., 2016). While we share our need for sleep with animals, the parallels may extend beyond the physiological imperative. Although the commitments that lead us to willingly sacrifice sleep seem so uniquely human, animals also face competing demands on their time that they need to balance with their physiological sleep requirement. Animals need to locate and move to suitable habitats, find and consume food and water resources, pursue mating opportunities, maintain social bonds, and care for young—all activities that are precluded, or rendered exceedingly challenging, by sleep (Capellini et al., 2010). Many animals face pressures on their sleep that are qualitatively different than those experienced by most modern humans. Notably, sleeping animals are highly vulnerable to their predators, rendering this state of reduced awareness potentially fatal for wild animals (Lima et al., 2005). Thus, animals face substantial trade-offs when investing in this costly, yet essential behavior, indicating that, for millions of years, evolution has honed—and continues to hone today—the strategies that animals employ in navigating these sleep trade-offs.

Sleep has evolved in a complex and dynamic environment, where its costs and benefits depend critically not only upon an ever-changing abiotic and phenological landscape, but also upon the presence and behaviors of other animals in the local ecosystem. Thus, the dynamics that result from the choices and activities of nearby animals may fundamentally shape an individual's decisions of when, where, and how to sleep. The presence of and exposure to heterospecifics, specifically predators, may strongly influence sleep investment, due to the vulnerability of sleeping animals to their predators (Lima et al., 2005). Indeed, individuals sacrifice sleep when sleeping in a position associated with a high risk of predation (Rattenborg et al., 1999a), or when experimentally exposed to a predator cue (Lesku et al., 2008; but see Stuber et al., 2014). These patterns at the individual level are mirrored at the species level, with taxa that are more vulnerable to the risk of predation (e.g. herbivores) typically experiencing shorter average sleep duration than less vulnerable species (e.g. carnivores; Capellini et al., 2008; Lesku et al., 2006). Optimizing the trade-off between sleep and predator avoidance may involve adjusting sleep investment according to the current risk of predation, which can vary over space and time (Lima et al., 2005; Preisser et al., 2005). However, pressures to forego sleep, or engage in particularly short duration, low intensity sleep, when at a high risk of

predation may often create direct conflicts with the physiological need for sleep and its homeostatic regulation.

The behavior of conspecifics may also modulate the costs and benefits of sleep, thus having an important influence on how individuals navigate their sleep trade-off. For the many animals that live and sleep in cohesive social groups, the safety provided by collective vigilance and predator dilution while sleeping with their group-mates may decrease the risks associated with this vulnerable behavior (Bednekoff & Lima, 1998; Lima et al., 2005; Wrona & Dixon, 1991). Staggered periods of wakefulness among group-mates may further reduce the costs of sleep by maximizing collective vigilance (i.e. the "sentinel hypothesis"; Samson et al., 2017). However, the social disruptions of sleep caused by the nighttime activity of nearby group-mates may present challenges to fulfilling a sleep imperative (Noser et al., 2003). Moreover, sleeping with group-mates may generate social opportunity costs of sleep, with sleep investment achieved at the cost of potentially engaging in the interactions with proximate group-mates. These interactions could prove important for developing and maintaining social bonds, which increase fitness (Cameron et al., 2009; Campos et al., 2020; Frère et al., 2010; Riehl & Strong, 2018; Silk, 2003; Silk et al., 2010). Indeed, an early phylogenetic analysis of sleep across mammal species found that social mammals sleep less than solitary mammals, and suggested that this pattern may reflect a trade-off between sleep and time devoted to servicing social relationships (Capellini et al., 2008). The exact costs and benefits aside, the influence of the social environment in modulating these costs and benefits of sleep may differ for each group-mate, as variation among group-mates in their intrinsic traits and the relationships they have with each other can shape how each individual experiences the collective dynamics of the group (Strauss & Shizuka, 2022). Thus, both the immediate social environment, as well as the positions of individuals within the networks that describe it, may influence how individuals negotiate their investment in sleep (Karamihalev et al., 2019).

The social environment, however, is not only limited to familiar group-mates. The density and distribution of distinct social groups (or individuals, for solitary species) across the landscape, as well as the spatio-temporal overlap in their space use, may further shape the costs and benefits that animals face when they sleep. Neighboring groups are typically in direct competition over resources

(Brown, 2013; Kitchen et al., 2004; Thompson et al., 2017), and, for the many animals that take refuge to mitigate the risk of predation or exposure to the elements while sleeping, groups may compete over access to high-quality sleep sites (Anderson, 1984; Markham et al., 2016). Even when distinct groups share a refuge, members of the groups may then compete over preferred sleeping locations within the shared refuge (Smeltzer et al., 2022). Whether direct or indirect, both competition over entire sleep refuges or ideal locations within the refuge may lead at least some members of the population to inhabit sub-optimal locations during their sleep period, with implications for the risks associated with sleep (Smeltzer et al., 2022). Competition between social groups in a shared refuge may present its own risks if interactions between groups are intensely hostile, with sleep leaving animals potentially vulnerable to conspecific attack (Nunn et al., 2016). When tolerant groups share a sleep refuge, costs of sleep may arise in a qualitatively different fashion; namely, sleeping together may increase the social opportunity costs of sleep. Inter-group interactions provide opportunities for dispersal and extra-group mating (Drewe et al., 2009; Lawler, 2007), which members of neighboring groups may prioritize over sleep when spending a night in a shared sleep site. Alternatively, congregating with another social group during the sleep period may actually decrease the costs of investing in sleep, with the increase in collective vigilance and predator dilution leading to a diminished risk of predation when sleeping with another group (Finkbeiner et al., 2012).

Overall, the evolutionary trajectory of sleep behavior may have been guided by many complex and dynamic ecological and social pressures. However, we know exceptionally little about how these ecologically and socially relevant contexts actually influence sleep patterns, or how animals navigate the trade-offs that arise from direct conflicts between their ecological and social priorities and their physiological sleep imperative. We know even less about how this need for sleep feeds back to shape the socioecology of a species. Thus, a sizeable gap in our understanding of one of the most universal animal behaviors has withstood almost a century of modern sleep science (Berger, 1931).

Logistical challenges that have limited the study of sleep to the laboratory have perpetuated this gap in our knowledge. Sleep research has relied almost exclusively on polysomnography—the gold standard in sleep research—to measure sleep patterns (Aulsebrook et al., 2016; Rattenborg et al.,

2017). Although recent technological developments have enabled exciting advances in the implementation of polysomnography in the wild (e.g. Rattenborg et al., 2016; Voirin et al., 2014; reviewed in Rattenborg et al. 2017), the relatively invasive nature of polysomnography largely constrains its use—and thus, the study of sleep—to the laboratory (Smeltzer et al., 2022). By studying sleep outside of the context in which it evolved, we risk misinterpreting key sleep adaptations and the adaptive value of sleep more broadly, and, in doing so, potentially overlook fundamental interdependencies between an animal's sleep physiology and its behavioral ecology.

My dissertation research introduces novel methods to bring sleep research into the wild, and uses these methods to shed new and important light on how the behavioral ecology of an animal both shapes and is shaped by its sleep physiology. I achieved this objective by asking and answering basic questions about how sleep manifests in the wild at three levels of biological organization that approximately align with the three chapters of this dissertation. Chapter 1 focuses primarily on the individual level, investigating how animals navigate trade-offs between their physiological need for sleep and the ecological and social pressures that render sleep costly in the wild. Chapter 1 also draws connections to the group level, by exploring collective signatures of sleep. Chapter 2 commences where Chapter 1 ends, at the group level, exploring how the collective dynamics within a social group shape sleep patterns of its members. This chapter takes a step further into the complexity of collective behavior by investigating how these collective sleep dynamics present in a highly structured society, in which variation among group members and the relationships they share with each other can influence the way each individual uniquely experiences the consequences of collective dynamics. Chapter 3 scales to the population level, examining how interactions between neighboring groups influence sleep patterns within a shared sleep site, and how the social dynamics within a shared sleep site feed back to influence subsequent interactions and the broader relationships between groups.

The olive baboons (*Papio anubis*) ranging near Mpala Research Centre in Laikipia, Kenya offered an ideal study system in which to investigate these research questions for three central reasons. First, despite taking refuge on rock outcroppings and trees for the night (Bidner et al., 2018; Markham et al., 2016), baboons remain highly vulnerable to nocturnal predation by leopards (Busse, 1980; Cowlishaw, 1994; Isbell et al., 2018). This nocturnal predation represents the main source of

mortality for adult baboons (Cheney et al., 2004), creating a fitness-critical trade-off between investing in sleep and engaging in anti-predator behavior. Mpala Research Centre, a 200 km^2 land conservancy, is home to a healthy population of leopards, with a recently recorded density of 12.03/100 km^2. As of 2015, the home ranges of at least seven leopards overlapped with the home ranges of the baboon groups in this study (L. Isbell, personal communication; Bidner et al., 2018; O'Brien & Kinnaird, 2011). Secondly, baboons live—and sleep—in stable, cohesive social groups, characterized by highly asymmetric kinship, affiliative, and dominance networks (Cheney & Seyfarth, 2008). An individual's position within these networks critically influences the way it experiences many aspects of group life, and thus, individuals invest heavily in maintaining their social relationships (Cheney et al., 2016; Silk et al., 2009). Lastly, baboon groups share large areas of home range overlap with neighboring groups (Bidner et al., 2018; Markham et al., 2016). This extensive overlap in their space use, combined with a scarcity of high-quality sleep refuges, leads distinct social groups to occasionally spend the night at the same sleep site (Bidner et al., 2018; Markham et al., 2016).

To shed light on the behavioral ecology of sleep in the wild, I measured the sleep of wild baboons using collar-mounted accelerometers. A recent dramatic rise in the availability and prevalence of human wearable technology has led to rapid progress in the development of algorithms that extract metrics of sleep from wearable accelerometers (Johnson & Picard, 2020). I adapted two such complementary algorithms that were originally developed to measure sleep for research in humans (van Hees et al., 2015, 2018), and used these adaptations to classify sleep behavior in wild baboons from data collected by collar-mounted accelerometers (Fig. 0.1). I validated this method of accelerometer-based sleep classification against direct observations of the sleep and waking behavior of collared baboons in the wild, leveraging high-resolution infrared imagery to facilitate these observations. I then applied the validated sleep classification algorithm to extract sleep patterns from three distinct datasets of accelerometry collected from baboons ranging near Mpala Research Centre, using a unique dataset for each chapter of this dissertation. By investigating the physiological, ecological, and social factors shaping and shaped by sleep in wild baboons with these datasets, my dissertation research is uniquely positioned to offer some of the first insights into the behavioral

ecology of sleep in social animal groups. Perhaps more importantly, this dissertation demonstrates the implementation of non-invasive, scalable tools that move sleep research from the laboratory to the wild, and, in doing so, creates exciting new opportunities to study sleep at unprecedented scales in the environment in which it evolved (Watanabe & Rutz, 2022).

Figure 0.1. Investigating the behavioral ecology of sleep in wild olive baboons. My dissertation research uses collar-mounted tri-axial accelerometry (x-axis: yellow, y-axis: blue, z-axis: red) to measure the fine-scale movements of wild baboons. With this complete record of movement, I algorithmically identified sustained periods of inactivity as sleep (sleep: blue-outlined accelerometry displays, waking: orange-outlined accelerometry displays), and performed direct observations of sleep and waking behavior of collared individuals in infrared imagery (inset) to validate the accelerometer-based sleep classification algorithm. These tools enabled me to study sleep in the wild, and thus, achieve significant advances in our understanding of the behavioral ecology of sleep. Artwork credit: Mike Costelloe, for the Max Planck Institute of Animal Behavior (CC-BY-NC-ND 4.0).

Chapter 1: Ecological and social pressures interfere with homeostatic sleep regulation in the wild

Abstract

Sleep is fundamental to the health and fitness of all animals. The physiological importance of sleep is underscored by the central role of homeostasis in determining sleep investment – following periods of sleep deprivation, individuals experience longer and more intense sleep bouts. Yet, most sleep research has been conducted in highly controlled settings, removed from evolutionarily-relevant contexts that may hinder the maintenance of sleep homeostasis. Using tri-axial accelerometry and GPS to track the sleep patterns of a group of wild baboons (*Papio anubis*), we found that ecological and social pressures indeed interfere with homeostatic sleep regulation. Baboons sacrificed time spent sleeping when in less familiar locations and when sleeping in proximity to more group-mates, regardless of how long they had slept the prior night or how much they had physically exerted themselves the preceding day. Further, they did not appear to compensate for lost sleep via more intense sleep bouts. We found that the collective dynamics characteristic of social animal groups persist into the sleep period, as baboons exhibited synchronized patterns of waking throughout the night, particularly with nearby group-mates. Thus, for animals whose fitness depends critically on avoiding predation and developing social relationships, maintaining sleep homeostasis may be only secondary to remaining vigilant when sleeping in risky habitats and interacting with group-mates during the night. Our results highlight the importance of studying sleep in ecologically relevant contexts, where the adaptive function of sleep patterns directly reflects the complex trade-offs that have guided its evolution.

Introduction

Sleep is an important and understudied facet of animal lives, with every species, from honey bees to humans, allocating a portion of each day to this period of rest (Cirelli & Tononi, 2008). The universality of sleep reflects its central role in important physiological processes, including memory consolidation, support of the central nervous system, energy conservation and physical restoration (Chowdhury & Shafer, 2020; Gangwisch, 2014; Stickgold, 2005; Vyazovskiy, 2015). Accordingly, failure to meet daily sleep demand has health consequences (Basner et al., 2013), with potentially

fatal repercussions of extreme sleep deprivation (Rechtschaffen & Bergmann, 2002). The physiological need for sleep is emphasized by its homeostatic control – after periods of insufficient sleep or extreme physical exertion, individuals experience particularly long and intense bouts of sleep (Kitamura et al., 2016). Decades of sleep research have consistently implicated homeostasis as a primary determinant of sleep patterns, such that homeostatic regulation has become an important criterion in the very definition of sleep (Siegel, 2008).

A strong focus on studying sleep in the laboratory or at the bedside, although revealing much about the physiology of sleep, has inherently overlooked the ecological pressures that drive the regulation and evolution of sleep (Rattenborg et al., 2017; Reinhardt, 2020). In the natural world, the significance of sleep extends beyond its direct physiological impacts. Sleeping animals typically cannot engage in other behaviors that are important to their survival (but see Lyamin et al., 2008, 2018; Rattenborg et al., 1999, 2016), and investing in sleep when environmental forces render vigilance and activity particularly important may impose substantial costs to wild animals. In addition to preventing animals from foraging, searching for mating opportunities, defending territories, and caring for young, sleep leaves animals in a state of extreme inattention, and thus highly vulnerable to their predators (Lima et al., 2005). The evolution of sleep and its manifestation in the wild may therefore be driven by a complex balance between the physiological need for sleep and ecological costs imposed on sleeping animals.

For gregarious animals, the balance between the costs and benefits of sleep may be further modulated by the social environment. However, even the most basic aspects of sleeping with conspecifics, such as whether the social context facilitates or constrains sleep, remain unknown (Karamihalev et al., 2019). Sleeping in a social context could alter the costs of sleep – the sentinel hypothesis suggests that staggering the timing of sleep bouts in a group can collectively maintain both high quality sleep and high levels of anti-predator vigilance (Samson et al., 2017; Snyder, 1966). Sleeping in a group may therefore facilitate an individual's ability to fulfill its physiological sleep requirement by reducing the risk of doing so. Alternatively, social dynamics may actually inhibit investment in sleep. Sleep may present social opportunity costs, causing individuals to sacrifice sleep in order to spend more time actively engaging with group-mates. Additionally, proximity to group-

mates may cause sleep disruptions initiated by short periods of wakeful activity of neighboring individuals. Cascading disruptions could then lead to collective dynamics of sleep, such as the waves of wakefulness that have been documented in flocks of gulls (Beauchamp, 2009, 2011). Thus, sleeping in close proximity to conspecifics may potentially be accompanied by both costs and benefits for an individual's ability to obtain sufficient sleep, and discovering how these potential costs and benefits are actually realized will shed light on the forces that have guided sleep adaptations in social animals.

To understand how group-living animals navigate trade-offs between their physiological need for sleep and the ecological and social pressures that shape the costs and benefits associated with this biological imperative, we investigated the factors shaping sleep patterns of wild olive baboons (*Papio anubis*). Baboons live in stable multi-male, multi-female groups of up to 100 individuals (Cheney & Seyfarth, 2008), and during the night, they seek safety in trees and rock outcroppings (Altmann & Altmann, 1970; Busse, 1980). Despite seeking refuge in these sleep sites, baboons remain particularly vulnerable to nighttime predation from leopards, which represents the single largest source of mortality for adult baboons (Cheney et al., 2004; Cowlishaw, 1994; Isbell et al., 2018). Baboons must therefore navigate the trade-off between investing in sleep and maintaining anti-predator vigilance. As a highly gregarious animal whose fitness depends heavily on their social relationships (Silk et al., 2009), baboons must also balance their time spent sleeping with their investment in social interactions, as time constraints during the day limit their ability to build and maintain their relationships (Dunbar, 1992).

We simultaneously tracked the activity of 26 wild olive baboons from the same group using collars fitted with GPS sensors and tri-axial accelerometers to understand how baboons manage their competing nighttime priorities. Accelerometer-based sleep classification has shown an impressive ability to detect and monitor sleep behavior across taxa (Ancoli-Israel et al., 2003; de Souza et al., 2003; Hoffmann et al., 2012; Ladha & Hoffman, 2018; Malungo et al., 2021; Qin et al., 2020), and is now commonly used to assess sleep in both humans (e.g. Jones et al., 2019; Patel et al., 2017) and non-human animals (e.g. Gravett et al., 2017; Reinhardt, 2020; Samson et al., 2018). Validation studies comparing performance of this non-invasive method to polysomnography—the gold standard

in sleep research—generally show high accuracy (78-90%; Ancoli-Israel et al., 2003; Kanady et al., 2011; Malungo et al., 2021; Shambroom et al., 2012), although concerns remain about the ability of movement-based methods to distinguish sleep from resting wakefulness (Ancoli-Israel et al., 2003; de Souza et al., 2003), and results must be evaluated with these caveats in mind. For this study, we adapted a well-validated sleep classification algorithm used in human research (van Hees et al., 2015; van Hees et al., 2018) and validated its ability to detect sleep in wild baboons. We then used this algorithm to describe the sleep patterns of members of our study group over a period of a month (Supplementary file 1a). We used these data to assess the influence of homeostatic regulation on the pattern of sleep and wake bouts within nights, as well as the duration and fragmentation of sleep across nights. We also leveraged naturally occurring sleep disturbances to test how recent sleep history influenced arousal threshold during sleep. We compared the influence of homeostatic regulation to that of the location in which individuals slept (both within the sleep site as well as between distinct sleep sites) and their local social environment, both of which may exert pressures on sleep behavior in the wild that conflict with the maintenance of homeostasis.

Results

The diel pattern of activity in wild baboons, as reflected by accelerometry data, reveals a clear monophasic sleep pattern, with individuals active during the day and inactive at night (Fig. 1.1B). To derive metrics of sleep (sleep onset time, awakening time, total sleep time, sleep period duration, sleep efficiency, sleep fragmentation), we calculated the log of the vectorial dynamic body acceleration (VeDBA), a widely-used measure of overall movement activity (Qasem et al., 2012), from 36 calendar days or 354 baboon-nights. Sleep onset occurred 53.0 ± 1.7 (mean ± SE) minutes prior to the end of evening astronomical twilight, and baboons awoke 35.9 ± 1.7 minutes after the beginning of morning astronomical twilight (Fig. 1.1A,C). The duration of the sleep period – the period between sleep onset and awakening – was 11.0 ± 0.04 hours on average. Within the sleep period, baboons slept for an average of 9.2 ± 0.04 hours (total sleep time), displaying an average sleep efficiency of 85.0% ± 0.2%. Baboons exhibited 1.8 ± 0.03 distinct wake bouts per hour of sleep during the sleep period (sleep fragmentation).

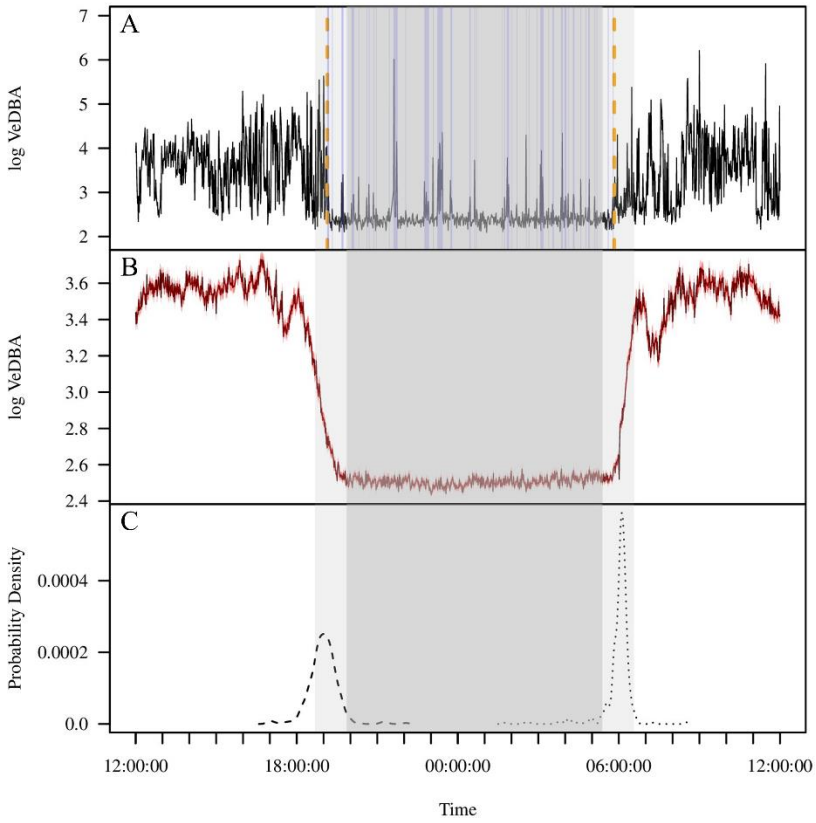

Figure 1.1. Extracting activity and sleep from accelerometry in a group of wild olive baboons. Adapting algorithms developed by van Hees and colleagues (2015, 2018), we used the vectorial dynamic body acceleration (VeDBA), a measure of overall activity, to determine the sleep onset and awakening times (A; orange dotted lines), as well as periods of wake after sleep onset (A; blue shading) for each individual baboon on each day. These metrics allowed us to calculate the total sleep time, sleep period duration, sleep efficiency, and sleep fragmentation as well. The plot (A) shows the data of one individual within a single noon-to-noon period as an example. Averaged across all individuals on all nights (N = 354 baboons-nights), the log VeDBA shows that baboons exhibit activity patterns typical of a diurnal animal with monophasic sleep (B), with a consolidated period of very low levels of activity during the night. Although the timing of waking (C; dotted line) was more consistent across the group and across the study period than the timing of sleep onset (C; dashed line), both sleep onset and waking typically occurred within astronomical twilight. The red shading in (B) indicates ± 1 SE. In all subplots, the grey shaded region depicts the period between sunset and sunrise, with double shading from the end of astronomical twilight to the beginning of morning astronomical twilight.

Due to high correlation of total sleep time with onset time, awakening time, sleep period duration, and sleep efficiency, as well as a strong relationship between sleep fragmentation and sleep

efficiency (Supplementary file 1b), we focused the majority of our analyses on total sleep time and sleep fragmentation. Individuals differed in their total sleep time and sleep fragmentation, and much of this variation reflected differences between the sexes and variation across age categories. Males slept an average of 20 minutes longer than females and experienced 0.23 fewer wake bouts per hour of sleep (total sleep time Linear Mixed Model (LMM): standardized estimate [95% credible interval lower bound, 95% credible interval upper bound]: 0.44 [-0.05, 0.94]; sleep fragmentation LMM: -0.44 [-1.04, 0.17]). Juveniles and subadults slept, on average, 16 minutes less and woke on 0.38 and 0.28 more occasions per hour of sleep, respectively, than adults (total sleep time LMM: juveniles: -0.34 [-1.15, 0.50], subadults: -0.34 [-0.81, 0.14]; sleep fragmentation LMM: juveniles: 0.72 [-0.28, 1.75], subadults: 0.52 [-0.06, 1.10]).

An individual's recent history of sleep and activity was not a strong driver of sleep patterns (Fig. 1.2, Figure 1.2-figure supplement 1, Figure 1.2-figure supplement 2). Neither total sleep time nor sleep fragmentation the previous night affected time spent napping the following day, time spent sleeping the following night, or the fragmentation of sleep the following night (Supplementary file 1f; time spent napping LMM: previous night total sleep time: 0.03 [-0.10, 0.17], previous night sleep fragmentation: 0.00 [-0.11, 0.12]; total sleep time LMM: previous night relative total sleep time: -0.04 [-0.19, 0.12], previous night relative sleep fragmentation: -0.06 [-0.19, 0.06], Fig. 1.2A*(ii)-(iii)*; sleep fragmentation LMM: previous night relative total sleep time: 0.09 [-0.10, 0.27], previous night relative sleep fragmentation: -0.03 [-0.18, 0.12], Fig. 1.2B*(ii)-(iii)*). However, after spending more time napping during the day, baboons did experience shorter total sleep time and more fragmented sleep during the night (Fig. 1.2A*(i*), Fig. 1.2B*(i*); total sleep time LMM: -0.19 [-0.36, -0.01], sleep fragmentation LMM: 0.22 [0.00, 0.45]). For every 10 minutes spent napping, baboons spent 6 fewer minutes sleeping the following night and woke 0.10 times more per hour of sleep. Neither sleep duration nor fragmentation were influenced by the distance baboons travelled (Fig. 1.2A*(iv*), Fig. 1.2B*(iv*); total sleep time LMM: -0.03 [-0.19, 0.14]; sleep fragmentation LMM: -0.04 [-0.13, 0.05]) or the VeDBA they accumulated during the day (Supplementary file 1e, 1l; total sleep time LMM: -0.12 [-0.34, 0.12]; sleep fragmentation LMM: -0.05 [-0.33, 0.23]).

In humans, homeostatic regulation of sleep manifests within, as well as between nights: sleep wanes and wakeful activity increases over the course of the sleep period as individuals gradually fulfill their sleep requirements (Winnebeck et al, 2018). Baboons, in contrast, did not demonstrate this pattern: their probability of being asleep did not decrease as the night progressed, despite exhibiting cyclic sleep patterns that are otherwise similar to patterns of human sleep (Fig. 1.2D; GAMM: r^2_{adj} = 0.008, $F_{(8.741)} = 89.16$, $p < 1x10^{-15}$).

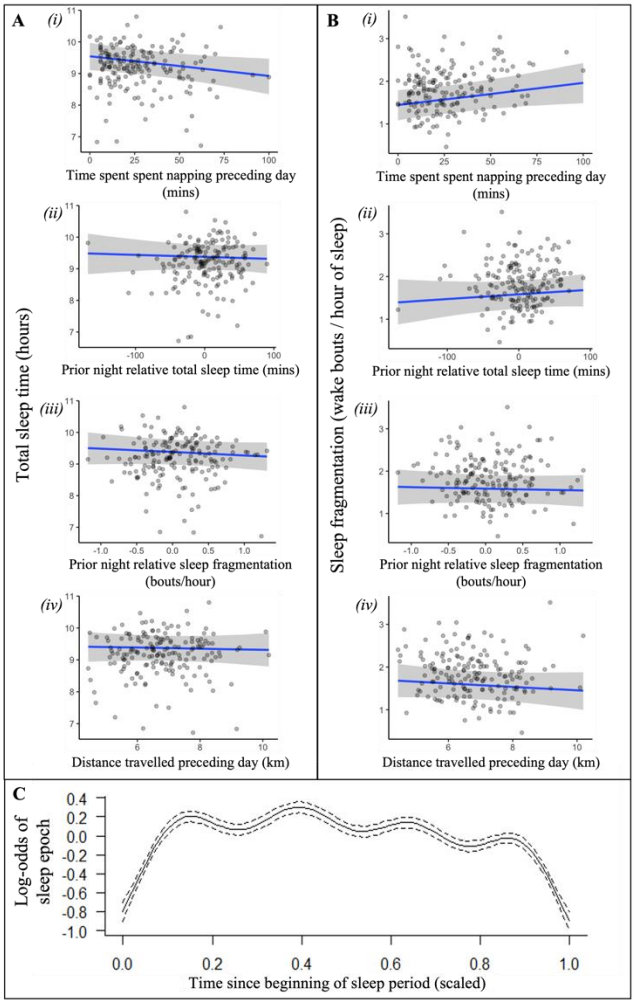

Figure 1.2. Recent history of sleep and activity has a weak influence on baboon sleep patterns. Neither the relative sleep time on the previous night, the relative sleep fragmentation on the previous night, nor the distance travelled on the preceding day influenced sleep duration (A*(ii)-(iv)*) or sleep fragmentation (B*(ii)-(iv)*), although baboons did sleep less (A*(i)*) and experience more fragmented sleep (B*(i)*) following days with more napping. Additionally, the likelihood of a baboon being asleep did not substantially decrease as the night progressed and the baboon payed off its sleep debt (C). In (C), time since the beginning of the sleep period is scaled from 0

(beginning) to 1 (end of the sleep period). Subplots depict conditional effects of each variable from models of the data, with raw data points overlaid.

The location where baboons slept had a strong influence on sleep duration, with individuals experiencing reduced sleep quality in less familiar locations. For the first 21 nights of the study, group members slept at the same site along the Ewaso Ng'iro River, distributed across ten adjacent yellow fever (*Acacia xanthophloea*) trees (Fig. 1.3A). Individuals showed high fidelity to particular sleep trees (Figure 1.3-figure supplement 1); one-tailed two-sample Kolmogorov-Smirnov test: $p < 1.0 \times 10^{-9}$), returning each night to one of the small set of available trees populated by the group. Not only did the choice of tree itself influence sleep duration (Supplementary file 1c – 1d, Figure 1.3-figure supplement 2), but the individual's familiarity with their selected tree impacted how much they slept. Baboons slept longer in trees to which they showed higher fidelity (Fig. 1.3C; LMM: 0.21 [0.05, 0.36]), with individuals sleeping up to 33.4 minutes longer in the tree to which they showed highest fidelity than in the tree to which they showed lowest fidelity. Baboons did not compensate for shorter sleep duration with less fragmented sleep when sleeping in non-preferred trees (LMM: -0.05 [-0.24, 0.14]).

During the 21st night of the study, we heard the snarls and growls of a large felid, followed by sustained baboon screams and alarm calls that were emitted from the study group's sleep trees at 20:55. After listening to recordings of the vocalizations of the large cats present at the study site, and because leopards are the only predators that readily attack baboons in their sleep site during the night (Busse, 1980; Cheney et al., 2004), we concluded that the commotion may have reflected a leopard attack. If a leopard did indeed attack the group, then the attack was unsuccessful, as all members of the group were present the next morning. Alternatively, it is possible that no attack occurred, and that the baboon screams and alarm calls were emitted simply in response to the leopard's presence in the area. On the day following this leopard's presence, the group moved to a less commonly used sleep site 1.5 km away (Fig. 1.3B). They remained at this sleep site for three nights before returning to sleep at their main sleep site. While the baboons showed no substantial change in their sleep duration or fragmentation on the night of the leopard encounter (Fig. 1.3D, Figure 1.3-figure supplement 3,

Figure 1.3-figure supplement 4; total sleep time LMM: -0.25 [-0.87, 0.39]; sleep fragmentation LMM: -0.32 [-0.96, 0.33]), they slept 72 minutes less and exhibited 0.50 more wake bouts per hour of sleep, on average, upon moving to the less familiar sleep site (Fig. 1.3D ; LMM: -1.52 [-2.15, -0.86]). This decrease in total sleep time and increase in fragmentation following the change in sites was limited to the first night in the new sleep site, after which sleep duration and fragmentation returned to normal (Fig. 1.3D; Figure 1.3-figure supplement 3, Figure 1.3-figure supplement 4).

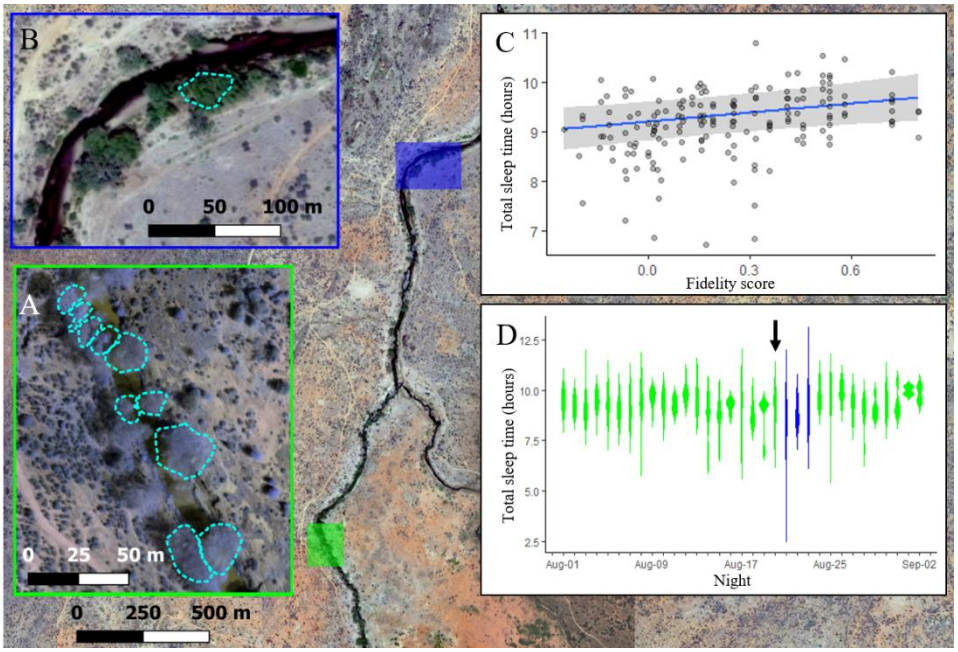

Figure 1.3. The location where baboons sleep has consequences for sleep duration. Group members spent the majority of the study (32/35 nights) sleeping in 10 yellow fever (*A. xanthophloea*) trees in a grove along the Ewaso Ng'iro river (A). Within this sleep site, baboons slept longer when sleeping in trees to which they showed high fidelity (C). At 20:55 on the 21st night of the study, the group detected a leopard near their sleep site sleep site. The following day, the baboons moved to a new sleep site 1.5 km away from their main sleep site (B). Baboons slept substantially less following this change in sleep site, but this effect did not persist beyond the first night in the new location (D). (C) depicts the conditional effects from models of the data, with raw data points overlaid, and (D) depicts a violin plot of the data, with color corresponding to the sleep site (A and B). The arrow in (D) indicates the night on which the group detected a leopard near their sleep site.

Sleeping in a social context also impacted sleep duration. Contrary to predictions of the sentinel hypothesis, the proportion of the night in which at least one individual was awake was significantly less than expected by chance (Fig. 1.4A; Fisher's exact test: $p < 0.0001$), suggesting that, rather than staggering periods of nocturnal wakefulness, group-mates were actually synchronized in their sleep-wake patterns throughout the night. Confirming this synchronization, we found that a significantly greater proportion of the group exhibited the same simultaneous behavior, either being asleep or awake, than expected (Fig. 1.4B, Figure 1.4-figure supplement 1, Fisher's exact test: $p < 0.0001$; Figure 1.4-figure supplement 2, Fisher's exact test: $p < 0.0001$). Moreover, pairs of baboons showed more synchronization when sleeping in the same tree than when sleeping in different trees (Fig. 1.4C; LMM: 0.56 [0.47 – 0.64]), which suggested that sleeping individuals may awaken in response to the activity of group-mates in their local environment, or that external disruptions in the local environment may simultaneously waken all group members in the vicinity. To distinguish between these potential explanations, we tested the influence of the number of group-mates in an individual's local environment on their total sleep time, and found that individuals slept less when sharing their sleeping tree with more group-mates (Fig. 1.4D; LMM: -0.53 [-0.87, -0.19]). Each additional tracked group-mate in a tree resulted in a 4.0-minute decrease in total sleep time. Individuals also appeared to experience more fragmented sleep when sleeping in the proximity of a greater number of group-mates, but large uncertainty in the model estimate prevents a definitive conclusion about the influence of the social environment on sleep fragmentation (LMM: 0.26 [-0.15, 0.67]).

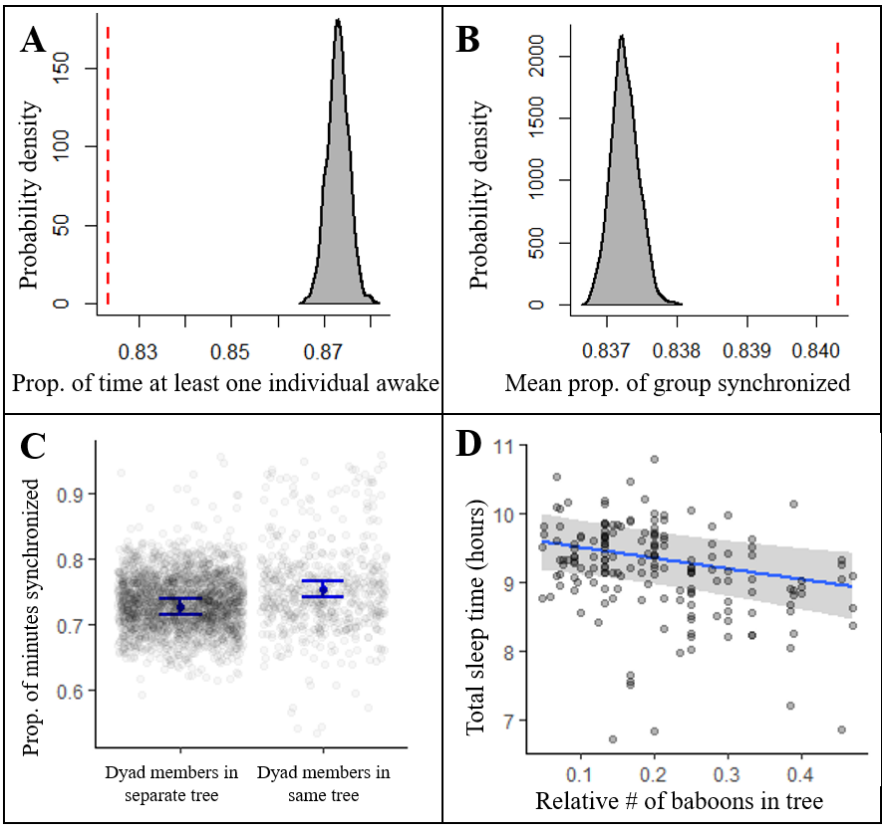

Figure 1.4. Collective dynamics within the sleep site influence sleep patterns. Group-mates' periods of nocturnal wakefulness were not staggered, but rather synchronized, as indicated by a significantly lower proportion of time with at least one individual awake (A, dotted red line; Fisher's exact test: $p < 0.0001$) and a significantly greater proportion of the group exhibiting synchronized behaviors (B, dotted red line; Fisher's exact test: $p < 0.0001$) than expected based on 1000 time-shifted data sets (gray distribution). Synchronized sleep patterns likely result from individuals waking in response to the nighttime activity of nearby group-mates, as dyads show greater synchronization when dyad members sleep in the same tree compared to when they sleep in different trees (C). As a consequence of these local social perturbations, baboons sleep less when sleeping in trees with more group-mates (D). Subplots (C) and (D) depict the conditional effects from models of the data, with raw data points overlaid.

Building on the evidence that co-sleeping baboons disrupt each other's sleep, we tested whether baboons maintain sleep homeostasis by sleeping deeper, rather than longer, following nights of poor sleep. Because sleep depth is measured by the amount of stimulation needed to awaken an animal (i.e. arousal threshold), we assessed sleep depth in situ by evaluating the probability of an individual waking in response to the activity of a neighboring group member. We found that although

individuals were indeed substantially more likely to wake following the awakening of others in their sleep tree, neither shorter duration nor more fragmented sleep the previous night dampened their responsiveness to group-mates (Bernoulli Generalized Linear Mixed Model (GLMM): influence of group-mate activity: 0.25 [0.16, 0.34], interaction between influence of group-mate activity and previous night relative total sleep time: -0.01 [-0.13, 0.11], interaction between influence of group-mate activity and previous night relative sleep fragmentation: -0.02 [-0.24, 0.21]).

We found no influence of moon phase or the minimum ambient temperature during the night on baboon sleep duration or fragmentation (total sleep time LMM: moon phase: 0.05 [-0.12, 0.22], temperature: -0.04 [-0.20, 0.13]; sleep fragmentation LMM: moon phase: -0.08 [-0.30, 0.13], temperature: 0.04 [-0.17, 0.26]).

Discussion

In this study, we demonstrate that the ecological and social demands that animals experience in the natural world can take precedence over the maintenance of sleep homeostasis. We show that while baboons sleep less in unfamiliar environments, and while their sleep is disrupted by the activity of group-mates, their recent history of sleep and physical exertion has only a limited role in influencing sleep behavior. Because baboons are highly vulnerable to nocturnal predation (Busse, 1980; Cheney et al., 2004; Isbell et al., 2018) and because they experience fitness benefits from maintaining strong social bonds (Silk et al., 2009), sacrificing sleep to maintain alertness in novel environments and to remain close to group-mates may represent critical adaptations. Our results highlight the trade-offs that group-living animals navigate when investing in sleep in the wild, and in doing so, challenge the centrality of the role that homeostasis has played in shaping sleep patterns in the environment in which sleep evolved. Decades of research in the laboratory and at the bedside have implicated homeostatic regulation as a key driver of sleep patterns, with the sleep rebound that follows periods of deficit facilitating the maintenance of a physiologically required amount of sleep (Amlaner et al., 2009). However, sleep studies have traditionally investigated sleep in highly controlled environments, where the costs of investing in sleep are largely absent. Our findings suggest that, in the natural world, “sleep need” may be a relatively flexible concept, with variation in sleep investment driven as much by the opportunity costs of sleep as by its physiological benefits.

There are substantial opportunity costs of devoting a significant portion of every day to sleeping. Sleeping animals are highly vulnerable to predation (Lima et al., 2005), and our results suggest that individuals sleep less when the risk of predation is particularly high. Baboon group members showed high fidelity to particular locations within their main sleep site, and individuals sacrificed sleep both when sleeping in non-preferred trees as well as upon moving to a new, less familiar sleep site following a leopard encounter. Given that predation risk tends to be greater in unfamiliar locations (Forrester et al., 2015; Gehr et al., 2020; Isbell et al., 1990, 1993; Isbell & Van Vuren, 1996; Yoder et al., 2004), baboons appear to trade sleep for vigilance according to the current risk of predation. Notably, however, we did not find that baboons decreased their investment in sleep on the night of the leopard encounter. This surprising result may indicate that baboons perceive uncertainty in the level of risk as potentially more dangerous than a confirmed threat. It is also possible that baboons did, in fact, sleep less following the leopard encounter, but remained exceptionally still, in a state of highly elevated vigilance. Because accelerometer-based sleep classification performs poorly in distinguishing motionless wakefulness from sleep, this state would likely have been falsely classified as sleep.

Engaging in sleep precludes investment in a variety of behaviors, in addition to anti-predator vigilance, that are important to fitness (Aulsebrook et al., 2016; Lesku et al., 2012; Lima et al., 2005; Roth et al., 2010). Consistent with our results, recent studies in ecologically-relevant contexts have revealed that animals forego sleep when ecological demands increase the associated opportunity costs. For example, while engaging in long, non-stop flights, great frigatebirds reduced the amount they slept by 92.7%, without apparent physiological consequences (Rattenborg et al., 2016). Similarly, male pectoral sandpipers greatly reduce their time spent sleeping during their short and intense mating season, and males that slept less actually experienced higher reproductive success (Lesku et al., 2012). Thus, across contexts and taxa, ecological pressures appear to supersede investment in sleep in the wild.

Animals might maintain homeostasis in the face of significant opportunity costs of sleep by sleeping more intensely, rather than longer, in response to elevated sleep need. Baboons in this study, however, did not appear to compensate in this way. We reached this conclusion using two distinct

approaches of inferring sleep depth from accelerometry data. First, we measured the fragmentation of sleep, which has been shown to correlate inversely with sleep depth (Bastuji & García-Larrea, 1999). Second, we directly assessed changes in arousal thresholds by tracking the propensity to wake in response to the nocturnal activity of neighboring group-mates. These approaches offer potentially promising avenues to expand our ability to non-invasively quantify the sleep behavior of animals in their natural habitats using accelerometry. However, validation against polysomnography – the gold standard for recording sleep – should be a priority for future work.

Recent technological advances allowing for the use of polysomnography in field conditions have played an important role in revealing the ecological trade-offs that wild animals face when navigating decisions about when, where, and how to sleep (Davimes et al., 2018; Lesku et al., 2011, 2012; Rattenborg et al., 2008, 2016; Scriba et al., 2013; Voirin et al., 2014). Although these advances hold great promise for wider application in the future, the invasive nature of polysomnography unfortunately limits its current use to taxa whose daily activities do not interfere with electrodes implanted either subdermally or inter-cranially. Because baboons are highly dexterous and engage in frequent allogrooming, we were unable to apply this gold standard, and instead, resorted to an alternate method to ask and answer important questions about the ecology of sleep in a wild social primate. Accelerometer-based sleep classification – a tool already used to investigate sleep across terrestrial (human: Jones et al., 2019; Patel et al., 2017; non-human: Bäckman et al., 2017; Davimes et al., 2018; Gravett et al., 2017; Lesku et al., 2011; Malungo et al., 2021; Qin et al., 2020; Reinhardt et al., 2019; Reyes et al., 2021; Samson et al., 2018; Sellers & Crompton, 2004; Sri Kantha & Suzuki, 2006; Suzuki et al., 2018) and marine taxa (Miller et al., 2008; Mitani et al., 2010; Wright et al., 2017) – offered a valid alternative to polysomnography. We note that the use of accelerometry can introduce biases in sleep monitoring, typically by overestimating total sleep time as a result of an inability to distinguish resting wakefulness from sleep (Ancoli-Israel et al., 2003; de Souza et al., 2003). Accelerometry is also limited in its ability to differentiate the stages of sleep (Conradt et al., 1997; but see Devine et al., 2021; Winnebeck et al., 2018). However, if these biases and limitations are considered during the interpretation of results, the use of accelerometry to investigate sleep provides an immediate opportunity to shed light on how diverse species balance their physiological sleep

requirements with ecological opportunity costs that vary according to natural history, trophic level, community composition, climate, and local environment. Further, the prevalence of accelerometer deployment in ecological research changes the scale at which sleep behavior can be studied, enabling the simultaneous and long-term monitoring of sleep at the population level. This rescaling of sleep research creates many new opportunities, one of which is the ability to record sleep in the majority of social group members and thus explore an exciting new scientific frontier: the collective dynamics of sleep.

Using accelerometry to track the sleep patterns of nearly an entire group of wild baboons, we demonstrated the importance of the social environment in shaping the sleep patterns of group-living animals. Contrary to the predictions of the sentinel hypothesis (Samson et al., 2017; Snyder, 1966), periods of nocturnal wakefulness of group members were not staggered, but rather synchronized, particularly with nearby group-mates. Baboons also slept less when in close proximity to a greater number of group-mates. Taken together, these results suggest that group-mates disrupt each other's sleep. Social disruptions may result from group-mates actively interacting with each other during the night. Gregarious animals often invest substantially in building and maintaining social relationships with their group-mates (Ward & Webster, 2016), and these bonds can prove essential to their fitness (Cameron et al., 2009; Campos et al., 2020; Frère et al., 2010; Riehl & Strong, 2018; Silk et al., 2009). Because animals have limited time to devote to maintaining their social bonds during the day (Dunbar, 1992), they may actively sacrifice sleep in order to invest in these relationships at night. Alternatively, social animals may wake in response to the periodic waking and repositioning of their group-mates during the night, and thus, socially-disrupted sleep is, perhaps, an inherent by-product of sleeping in a group. Simply remaining in a cohesive group may therefore present a challenge to obtaining sufficient sleep.

Social animals may jeopardize sleep homeostasis to maintain cohesion with their conspecifics because remaining in close proximity to their group-mates during the sleep period could prove essential to their fitness. Individuals likely benefit from the dilution of predation risk that is achieved through group cohesion, particularly when they are sleeping and thus highly vulnerable to predators (Lehtonen & Jaatinen, 2016). Collective vigilance may also reduce the risk of predation for group

members. Even in the absence of collective vigilance optimization via non-randomly staggered wakefulness, the proportion of the night with at least one group member awake is still likely to be substantially greater than any particular individual's investment in vigilance. In our study, at least one individual in the group was awake for 394 ± 11 minutes (82% ± 2%) from 21:00 to 05:00, although each individual was only awake for 79 ± 1 minutes (16% ± 0.2%) of the same period. Samson and colleagues (2017) found high levels of collective vigilance during the night in a group of Hadza hunter-gatherers, and they suggest that this collective vigilance may facilitate higher intensity sleep (Samson & Nunn, 2015). Future studies leveraging the indices of sleep depth that we applied in this study or advances in polysomnography (i.e. EEG) that may eventually allow its application in wild social animals could enable a test of this possibility.

Unexpectedly, we found that adult baboons slept longer than subadults and juveniles, and males slept longer than females. This contrasts with previous research that found age differences in sleep patterns linked to physiological demands during the development of the central nervous system (Amlaner et al., 2009) and sex differences in sleep tied to the influence of sex steroids (Mong & Cusmano, 2016), with younger individuals sleeping more than older individuals (Knutson, 2014; Ohayon et al., 2004; Olds et al., 2010; Steinmeyer et al., 2010; Stuber et al., 2015) and females sleeping more than males in birds and humans (Lendrem, 1983; Mong & Cusmano, 2016; Roehrs et al., 2006; Steinmeyer et al., 2010; Stuber et al., 2015). Our surprising results here may have been caused by biases in our study sample. The bio-logging collars were too heavy to mount on young juveniles and infants – the individuals that we would have predicted to sleep the most, due to their rapidly developing central nervous system (Frank, 2020; Frank & Heller, 2019). Thus, there may have been an overall decrease in time spent sleeping with age that we were unable to observe because we did not collect data on the youngest individuals. This result may also be an artefact of the tendency of accelerometer-based sleep monitoring to classify resting wakefulness as sleep (Supplementary file 1r; Ancoli-Israel et al., 2003; de Souza et al., 2003). Older individuals may rest quietly when waking during the night, thus falsely determined to be asleep according to their accelerometry, whereas younger individuals may be more likely to resume activity upon waking. However, if these findings are not the result of a bias in our study subject inclusion or sleep recording technique, they may reflect

variation in the vulnerability to predation among the age-sex classes in this highly sexually dimorphic species (Cheney et al., 2004), with young and female baboons likely realizing a higher cost of sleep than adult males. Individuals may also differ in their sleep patterns due to their ability to gain access to a high-quality sleep location within the group's sleep site. Our results have demonstrated the importance of location to sleep. However, group-mates may differ in their access to preferred sleep locations, particularly if preferred locations are limited. Baboon groups are structured by linear dominance hierarchies that shape the priority of access to resources (Cheney & Seyfarth, 2008; King et al., 2009; Marshall et al., 2015), and individuals can leverage their affiliative and kinship relationships to obtain resources that they would not be able to access based on social rank alone (Sick et al., 2014). Further research is needed to investigate the extent to which these complex social dynamics influence an individual's ability to obtain a preferred sleep location and, thus, a good night's sleep.

In addition to highlighting social dynamics as a key driver of sleep patterns in group-living species, our study provides important insights into selective pressures that may have shaped the evolution of human sleep. The physiological requirements for sleep and the homeostatic mechanisms that ensure this requirement is fulfilled have long been assumed to be the key drivers influencing the way that our sleep has evolved and the characteristics of our sleep today. However, we suggest that the criticality of homeostatic control in shaping our sleep patterns could be an artefact of sleeping in an environment devoid of the ecological and social costs that sleep would have presented our ancestors. Evidence suggests that, like baboons, early hominins were extremely vulnerable to nighttime predation in their dry savannah habitats (Brain, 1983; Treves & Palmqvist, 2007; Wrangham & Carmody, 2010). Hominins likely remained vulnerable to nocturnal predation until they began to manipulate fire, around which they could sleep to reduce the risk of predation (Samson & Nunn, 2015), and some characteristics of our sleep today may be best explained in light of the vulnerability that sleep imparted on our ancestors. For example, modern humans exhibit decreased sleep quality when sleeping in an unfamiliar environment (Tamaki et al., 2016), similar to the baboons in our study. The lower quality sleep resulting from this aptly named "first night effect" is limited to the first night in a new location (Tamaki et al., 2016), and our findings suggest that the first

night effect may be conserved from an environment where this first night would have been accompanied by poor information about risk. Early hominins would have also experienced a social opportunity cost of sleep, as they likely slept in groups (Samson & Nunn, 2015; Willems & van Schaik, 2017) and would have experienced constraints on the time available to maintain their social network during the day, until developing the advanced cognition that enabled a more efficient use of time (Nunn & Samson, 2018; Samson & Nunn, 2015). While our sleep has likely evolved substantially from that of our earliest ancestors, with modern human sleep being extremely short and intense compared to that of other primates (Nunn et al., 2016; Nunn & Samson, 2018), a full understanding of the way we sleep involves considering not only the physiological benefits of sleep, but also its ecological and social costs in the environment in which it evolved.

Materials and Methods

Data collection

We monitored sleep and activity patterns in a group of olive baboons at Mpala Research Centre, a 200 km^2 conservancy located on the Laikipia Plateau in central Kenya. We trapped and anesthetized 26 individuals, which comprised more than 80% of the adults and subadults in the study group (see Strandburg-Peshkin et al., 2015 for details on capture methodology). Upon capture, we noted the age class and sex of each baboon, as well as whether the baboon was lactating. We fit each individual with a GPS and accelerometry collar that recorded the baboon's GPS location at 1 Hz sampling interval and continuous tri-axial accelerations at 12 Hz/axis from 06:00 to 18:00. From 18:00 to 06:00, the collars recorded a 2.5-second burst of accelerations at 10 Hz/axis at the beginning of every minute. The collars were programmed to collect data from August 1, 2012 to September 6, 2012, but due to a programming glitch, several collars stopped collecting data prematurely (Supplementary file 1a). In total, we collected 483 days of GPS data, and 506 nights of accelerometry data. We also collected high-resolution drone imagery of the group's most commonly used sleep site (see Strandburg-Peshkin et al., 2017 for details).

While downloading data from the collars during the night of August 20, 2012, we heard the snarls and growls of a large felid, followed by sustained baboon screams and alarm calls that were emitted from the study group's sleep site at 20:55. Upon comparison of the vocalizations to

recordings of felids at the study site, we found that the vocalizations were most similar to the those of a leopard. Leopards are also the primary predator of baboons, and the only felid predator that readily attacks baboons in their sleep trees (Busse, 1980; Cheney et al., 2004; Cowlishaw, 1994; Isbell et al., 2018). We therefore presumed that the vocalizations were emitted by a leopard that had launched an attack on the group. Although we were only 45 m away from the nearest sleep tree, we were unable to make any direct visual observations of either the predator or the baboons during the presumed attack, due to the low-light conditions (sunset had occurred at 18:41). The following morning, a group count revealed that all group members were present and alive. We therefore concluded that the attack had failed. However, we note that it is also possible that the baboons' screams and alarm calls were simply a reaction to the presence of a leopard in the area that was not actively hunting, and that the study group therefore encountered a leopard, but was perhaps not attacked by the leopard.

Sleep Analysis

We used the accelerometry data to classify sleep behavior by adapting a method presented in van Hees et al. 2018 that was developed for extracting metrics of sleep in humans from wearable accelerometry devices. The process of determining the sleep period, defined as the period from sleep onset to waking, is summarized in Fig. 1.5.

To uniformize the accelerometry sampling schedule, we down-sampled and interpolated the daytime accelerometry data such that it matched the 10 Hz bursts of accelerometry collected during the night. We calculated the vectorial dynamic body acceleration (VeDBA) using a 0.7-second time-window and generated the log of the average VeDBA for the 2.5-second burst each minute. We then calculated a rolling median of the log VeDBA with a 9-minute window. Following van Hees et al. 2018, continuous periods of at least 30 minutes during which the rolling median of the log VeDBA was less than the 10^{th} percentile of the log VeDBA multiplied by 1.125 were considered sleep blocks. Any blocks within 45 minutes of each other were merged into sleep periods. If this resulted in more than one sleep period, the longest sleep period in the day, defined as a noon-to-noon period, was considered the sleep period. The beginning and end of the sleep period represents the time of sleep onset and waking, respectively. Of the 506 baboon-nights of accelerometry data, we successfully calculated the sleep period for 491 baboon-nights.

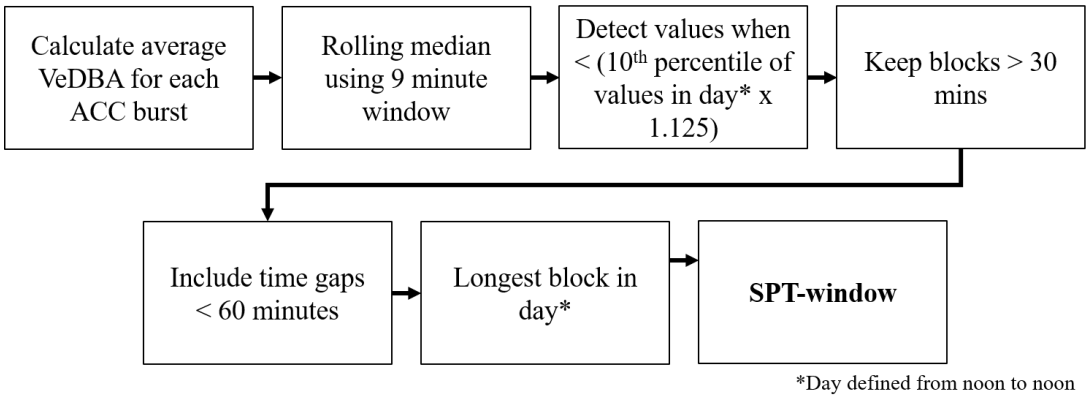

Figure 1.5. SPT-window detection algorithm adapted from Figure 1 in van Hees et al., 2018.

Adapting the method developed by van Hees and colleagues (2015), we classified each minute epoch both within and outside of the sleep period as representing either sleep or waking behavior. As above, the 10th percentile of the log VeDBA multiplied by 1.125 served as the classification threshold, and we classified epochs as indicating sleep when the log VeDBA for at least three consecutive epochs was below the log VeDBA threshold value. We classified all other epochs as representing waking behavior. Consistent with previous sleep analyses, we measured total sleep time as the total number of minutes of sleep epochs during the sleep period. We measured sleep efficiency as the total sleep time divided by the duration of the sleep period. We calculated sleep fragmentation as the total number of distinct wake bouts (i.e. separated by at least three epochs of sleep) within the sleep period that were greater than or equal to two minutes in duration, divided by the total sleep time, following (Samson & Nunn, 2015). We measured sleep time during the day – time spent napping – as the number of minutes of sleep epochs from 07:30 to 17:30, as these times were reliably within the waking period (Fig. 1.1C), and using standardized times prevented a spurious negative correlation between time spent sleeping during the waking period and total sleep time during the sleep period that would result from the waking period prior to or following short sleep periods having a greater number of potential epochs that could be considered sleep.

The accelerometer units occasionally failed to collect data according to their programmed sampling schedule. Because insufficient data in a given day would prevent a reliable calculation of the

threshold value for the sleep classification and produce variability in the number of potential sleep epochs, we did not include data for the sleep period time, sleep onset time, waking time, total sleep time, sleep efficiency, sleep fragmentation, or napping time (both on the prior day and following day) from noon-to-noon periods missing at least 120 (8.3%) accelerometry bursts, which decreased the number of baboon-nights from 491 to 368. We further removed data for the sleep period time, sleep onset time, waking time, total sleep time, sleep efficiency, and sleep fragmentation from noon-to-noon periods missing at least 20 consecutive accelerometry bursts, as the determination of the sleep period is sensitive to gaps between consecutive accelerometry bursts, resulting in a final number of 354 sleep periods analyzed. We did not remove data for napping time on these days because measuring napping time did not depend on the determination of the sleep period.

Validation of sleep classification algorithm

The algorithm from which the sleep classification technique is adapted is well-validated using polysomnography (C-statistic = 0.83 – 0.86) to both classify sleep behavior and determine the sleep period in humans (van Hees et al., 2015, 2018). Although the classification of sleep in non-human primates using devices and algorithms that were validated with polysomnography only in humans has become a common practice in sleep research (Barrett et al., 2009; Brutcher & Nader, 2013; Reinhardt et al., 2019; Reyes et al., 2021; Samson et al., 2018; Sri Kantha & Suzuki, 2006; Zhdanova et al., 2002), we returned to the study site in July 2019 to validate the accelerometer-based sleep classification. Because logistical and ethical limitations prevent the use of polysomnography in free-ranging, highly dexterous animals, we compared the accelerometer-based sleep classification to direct observations of wakeful and sleeping baboons fit with accelerometer collars for validation, as suggested by Rattenborg and colleagues (2017). Behavioral observations were facilitated by high-resolution infrared imagery (FLIR T1020, FLIR Systems Inc., Wilsonville, OR, USA). The validation study determined that our accelerometry-based classification of sleep exhibits an 80.7% accuracy (Supplementary file 1r; see Supplementary file 1 for further details of validation study).

Physical activity

Using the GPS data, we calculated each individual's daily travel distance. To avoid accumulation of GPS positional error overestimating the actual daily travel distance, we calculated

daily travel distance only after discretizing the GPS data to 5-meter resolution (Strandburg-Peshkin et al., 2017). We removed travel distance data on days on which a baboon's GPS collar first began taking fixes later than 07:30 or took its last fix before 17:00. Between these times, the group was often on the move, and thus delayed onset and premature offset of GPS devices that infringed upon this period would likely underestimate travel distances. We further removed one individual's data from the first half of the study due to a temporary collar malorientation that resulted in exaggerated GPS error.

We also calculated cumulative activity during the day from the accelerometry data. Using the continuous 12 Hz accelerometry data, we calculated VeDBA from 06:00 to 18:00 using a 0.5 second time window, averaged VeDBA over each minute, and then summed these values to generate a cumulative measure of activity during the day.

Sleep location characterization and fidelity

Visualization of the GPS data indicated that individuals remained reliably stationary until at least 06:15 every day, and thus we determined the location in which each baboon slept from the median of the first 10 GPS locations that occurred before 06:15. If an individual's GPS collar did not successfully collect 10 locations before 06:15, its data on this day were excluded from analyses involving sleep location. This resulted in the removal of 9/483 baboon-days of data. In ArcGIS, drone imagery was used to trace the crowns of distinct sleep trees within the group's main sleep site. We determined that an individual slept in a particular tree if its sleep location was within the traced polygon of that tree crown. Sleep locations that fell outside the crown of a tree, likely reflecting minor error in the GPS location estimates, were assigned to the closest sleeping tree. Only 32/469 sleep locations (6.8%) had to be assigned to a sleep tree in this manner. In rare cases where an individual's sleep location was greater than 10 m from the crown of the closest sleep tree (5/474 cases – 1.1% of baboon-days), its data on this day were excluded from analysis.

Analysis of the sleep location data revealed that, over the course of the study, the baboons slept in two distinct sleep sites that were separated by approximately 1.5 km. The group slept at their main sleep site for the first 21 nights of the study, and then spent three nights in a different sleep site after the leopard encounter on the 21st study night. The group then returned to the main site for the

duration of the study. In total, they spent 32/35 (91.4%) nights at their main site and 3/35 (8.6%) nights at the alternate sleep site. While the entire group slept in a single tree at the less frequently used sleep site, the group's main sleep site contained 10 trees across which the group slept. We performed a permutation test to investigate whether individuals exhibited consistency in the tree in which they chose to sleep. We calculated the Shannon entropy of each individual's sleep tree usage, and we compared these Shannon entropies to those produced from each of 1000 random exchanges of the locations of individuals on each night. Permuted values provide a null distribution controlling for potential sleep tree usage, as the distribution of individuals across the sleep trees each night from the empirical data was maintained in the permuted data. Shannon entropy is a measure of the uncertainty of a random variable, and is given by the equation:

$$H(X) = -\sum_{X=x} p(x)log\big(p(x)\big)$$

Thus, a lower Shannon entropy in the empirical data compared to the permuted data in this context would signal sleep tree fidelity, with an individual sleeping more often in certain trees and less often in other trees than expected by chance. To determine whether the baboons exhibited significant sleep tree fidelity, we compared the distribution of the group's empirical entropies to the distribution of entropies produced from the permutations with a one-tailed two-sample Kolmogorov-Smirnov test. As determining fidelity requires several nights of data, we did not include entropy values, either empirical or permuted, from individuals with less than four nights of data. We also limited this analysis of tree fidelity to the first 14 days of data, as the number of individuals on which we have data decreases sharply after this day (Supplementary file 1a), which decreases the possible permutations.

After determining that individuals showed non-random sleep tree selection (see Results), we then calculated an individual-specific fidelity index for each tree. This fidelity index was measured as the average number of nights an individual slept in a particular tree in the 1000 permutations subtracted from the number of nights the individual actually slept in that particular tree. Again, we did not calculate fidelity indices for individuals with less than four nights of data.

Pattern of sleep-wake behavior across the group

We tested whether individuals staggered their periods of nocturnal wakefulness or, conversely, synchronized them beyond the level expected by chance. For this analysis, we subset the data to times between 21:00 and 05:00, as these times consistently fell within the bounds of the sleep period of all individuals. We calculated the proportion of minute epochs across all nights in which at least one group member was awake and the proportion of the group that was synchronized in their behavior (either sleep or wakefulness) during each minute epoch, averaging across all epochs. We then calculated these same proportions, but after applying a random time shift to each individual's time series of sleep-wake epochs on each night (Figure 1.4-figure supplement 1). We repeated this procedure 1000 times to develop a null distribution of the proportion of epochs during the night in which at least one individual is awake and a null distribution of the average proportion of the group that was synchronized, and we compared the empirical proportions to their respective null distributions statistically with a Fisher's exact test. The p-value thus represents the proportion of time-shifted values that were as extreme or more extreme than the empirical value. Shifting the data in time rather than permuting it allowed us to develop null distributions while maintaining the autocorrelation structure of the data.

To confirm the robustness of our findings, we again tested for collective vigilance and synchronization, comparing the empirical values defined above to null distributions produced using an alternative method. In this method, rather than applying a random time shift to each night of each individual's data, we maintained the real time associated with the time series data, but we permuted the night associated with each time series (Figure 1.4-figure supplement 2). This permutation method controlled for the possibility that baboons exhibited synchronized sleep patterns simply due to a stereotyped schedule of activity that happened to be consistent across baboons and across nights. We compared empirical values to the null distributions created by these night permutations with a Fisher's exact test.

Statistical analysis of sleep

Data were processed using the statistical analysis software R version 4.0.5 (R Core Team, 2021). We only included the first 20 study nights in the analyses of sleep, except where specified, due to concerns that the leopard encounter that occurred on the 21st night could potentially disrupt typical

sleep patterns. To compare the effects of various physiological, ecological, and social predictors of sleep, we modeled total sleep time and sleep fragmentation with Bayesian linear mixed models (LMM), with random effects of individual identity and night, and fixed effects of age, sex, distance traveled in the preceding day, napping time during the preceding day, relative time spent sleeping the previous night, relative sleep fragmentation the previous night, identity of the sleep tree, fidelity index for the current sleep tree, relative number of individuals in the sleep tree, phase of the moon, and minimum ambient temperature during the night. We created a separate model that included cumulative VeDBA instead of distance travelled because cumulative daytime VeDBA was highly correlated with distance travelled during the day. An individual's relative time spent sleeping the previous night was measured as the difference between its total sleep time on the previous night and its average total sleep time. This relative measure controlled for positive correlations between total sleep time on the previous night and current night total sleep time that would result purely from among-individual variation in total sleep time – a scenario that would not be sufficiently controlled for by the individual identity random effect in this model. An individual's relative sleep fragmentation on the previous night was calculated for the same motivation. We calculated the relative number of individuals in the sleep tree by dividing the number of individuals in the sleep tree by the total number of individuals who were successfully assigned to a sleep tree on that given night, to control for the decrease in the number of individuals in each sleep tree over the course of the study that resulted from premature termination of data collection in several collars. Moon phase was a continuous variable realizing values from 0 to 1 (with 0 representing a new moon, and 1 representing a full moon), and we collected this data for the days of the study using the "sunCalc" package in R (Benoit & Elmarhraoui, 2019). The minimum ambient temperature represented the minimum temperature at the sleep site during the night, determined using interpolated ECMWF air temperature (2 m above ground) data obtained with the Env-DATA functionality (Dodge et al., 2013) provided on Movebank data repository (www.movebank.org). We standardized all response and predictor variables to allow for comparison of effect sizes among variables. To increase the interpretability of the total sleep time and sleep fragmentation models, we reran the models without standardized variables. Effect sizes reported in the main text are derived from the standardized models, whereas figures produced in the main text,

as well as the interpretation of the effect of each variable on the unstandardized sleep time are derived from the models with unstandardized variables.

To examine the effect of the leopard encounter and subsequent sleep site change on sleep parameters, we modeled the effect of particular nights on sleep parameters with Bayesian LMMs. Specifically, we divided data into the following categories: all nights before the leopard encounter, the night of the leopard encounter, the first night in the new sleep site (i.e. the night following the leopard encounter), the second night in the new sleep site, the third night in the new sleep site, and the remainder of study nights, during which the group slept in its main sleep site. Aside from this categorical night variable, we also included age, sex, distance traveled in the preceding day, napping time during the preceding day, relative time spent sleeping the previous night, relative sleep fragmentation the previous night, phase of the moon, and minimum ambient temperature as fixed effects in the models with random intercepts for individual identity. In these models, we did not include sleep tree identity, number of individuals in the sleep tree, and sleep tree fidelity score, as the entire group slept in a single tree in the less commonly used sleep site.

We further tested for the effect of prior sleep debt on sleep behavior by modeling the effect of total sleep time and sleep fragmentation on time spent napping the following day. We modeled this relationship with a Bayesian LMM, using individual identity and day as random intercepts. We also assessed how the likelihood of sleep progressed through the night. We used a generalized additive mixed model (GAMM) to model the log-odds of a baboon being asleep in a given epoch as a function of the duration of that epoch from the beginning of the sleep period, scaled such that 0 represents the beginning of the sleep period and 1 represents the end of the sleep period. We included individual identity and night as random intercepts, and to account for autocorrelation in the response variable, we also included an AR1 term in the model.

We tested whether individuals showed higher synchronization of their sleep-wake patterns when sharing the same sleep tree than when inhabiting different trees. With a Bayesian LMM, we modeled the synchronization score between dyads on each night, calculated as the number of minutes from 21:00 to 05:00 in which members of the dyad exhibited the same behavior divided by the total number minutes in which both individuals had data. We included a binary predictor variable

indicating whether dyad members were in the same tree as the only fixed effect variable, and night, the identity of both individuals in the dyad, as well as the identity of the dyad as random intercept variables.

To assess whether baboons experience deeper sleep following nights of poor sleep, we analyzed baboons' arousal thresholds as a function of their total sleep time and sleep fragmentation on the previous night. We leveraged the results of our previous analyses, which suggested that baboons may wake in response to the nighttime activity of their group-mates, and tested how their response to the nocturnal awakening of group-mates in their sleep tree is modulated by their previous night's sleep. We used a Bayesian Generalized Linear Mixed Model (GLMM) of family Bernoulli to model the log-odds of a focal baboon being awake in a given epoch as a function of a binary variable indicating whether any group-mate in the focal baboon's sleep tree was awake in the previous epoch, the focal baboon's relative total sleep time on the previous night, the focal baboon's relative sleep fragmentation on the previous night, and interactions between each of the previous night sleep variables and the binary variable indicating group-mate activity. We included random intercepts for individual identity and night. Because this analysis depended on knowing the location and sleep-wake state of group-mates and because many of the collars ceased collecting data after the 14th day of data collection, we limited this analysis to the first 14 nights of data collection. We only analyzed epochs between 21:00 and 05:00 as we were aiming to assess arousal thresholds well within the sleep period, rather than those at onset or during waking. Lastly, we further subset the data to be modelled to the epochs in which the focal baboon had been asleep for the three preceding epochs, as we were only interested in the response of sleeping baboons, and not baboons that were already awake, to external stimuli (i.e. their group-mates, in this case).

We carried out all Bayesian analyses with the "brms" package in R (Bürkner, 2017). We used diffuse, mean-zero Gaussian priors for all predictor variables. Model estimates are based off of four independent Hamiltonian Monte Carlo chains with 5000 iterations, 2500 of which were burn-in iterations. Trace plots indicated that mixing was sufficient and that the four chains converged on the same posterior region. Model estimates reported in the text represent the mean of the posterior distribution, along with the lower and upper 95% credible interval bounds from the standardized

models. We used package "mgcv" in R (Wood, 2011) to fit the GAMM to the sleep epoch data, using a thin plate spline smoothing term with 10 knots.

Evaluation of potential biases

In this section, we evaluate potential biases and limitations to the generalizability of our results, utilizing the STRANGE framework (Webster & Rutz, 2020).

(i) Social background:

Because all study subjects were free-ranging, wild baboons living in a group with a size and sex ratio that is typical for the species (study group size vs. typical group size: 46 vs. 15 – 100 (Ray & Sapolsky, 1992), study group sex ratio vs. typical sex ratio (males:female): 3:5 vs 1:2 (Barton et al., 1996)), we do not believe that the social background of the study individuals limits the generalizability of our findings to other baboon groups. Because we trapped and collared ~80% (24/29) of the adults and subadults in the study group, we believe that baboons with a wide variety of social statuses are represented in our data, and thus the results generalize well to other groups of baboons.

(ii) Trapability and self-selection:

We chose the study group based on the group's size, their proximity to an ideal trapping location, our ability to remotely download collar data from an infrequently used road near their main sleep site, and our avoidance of territorial conflicts with resident primatologists. Although we aimed to study a group that was relatively small, the study group was only slightly, if at all, smaller than other groups in the area. Thus, we do not feel that these selection criteria biased our results. Because we needed to trap individuals before collaring them, bold individuals, which tend to be more likely to enter traps (reviewed in Biro & Dingemanse, 2009), may be overrepresented in our data. To mitigate this bias, we manually triggered traps such that we could capture individuals that were hesitant to enter traps and may have only entered the traps once, rather than repeatedly capturing individuals that continuously entered traps. Capturing a large majority of adults and subadults in the group also helped to ensure representation of a wide range of behavioral types. Despite these mitigating measures, the baboons that we were unable to capture likely represented a non-random sample. However, research on behavioral syndromes suggest that these presumably shy individuals also tend to be more reactive

to external stimuli (Réale et al., 2010). We therefore predict that the individuals that we did not capture may have shown even more pronounced social and risk-related disruptions of sleep than those individuals included in our data, and thus, our conclusions should be unaffected by trapability bias. We were able to recover all data collected by the collars, and therefore, data recovery did not create any bias.

Although not trapability bias *per se*, we did not capture and collar any young juveniles or infants, as they were too small to carry the GPS/accelerometry collars. This bias certainly could have contributed to our surprising finding that adults slept more than younger individuals, as the youngest individuals, which would have been predicted to sleep the most, were excluded from our study.

(iii) Rearing history:

All study individuals were wild, and because they were only semi-habituated, they had relatively limited exposure to humans.

(iv) Acclimation and habituation:

Abnormal proximity to humans shortly prior to and during trapping, as well as handling and sedation directly associated with collaring, may have induced high levels of stress for study subjects. Because stress influences sleep (Han et al., 2012; L. Sanford et al., 2014), our procedure could have theoretically biased our results. However, our observations of baboons before and after trapping (both during this study and beyond) suggest that they continue normal behavior very shortly after trapping, and that they acclimate to the bio-logging collars almost instantly. Nonetheless, to ensure that study animals had acclimated to their collars and resumed normal behavior before commencing data collection, we delayed the start of data collection until three days after the last baboon had been trapped and collared. The majority of study individuals (~70%) were collared at least nine days before data collection commenced (Supplementary file 1a). Thus, we do not believe that study procedures biased our results. In confirmation, sleep patterns in the first few days of data collection were not abnormal (Fig. 1.3D).

(v) Natural change in responsiveness

Because our study took place near the equator, at a site with relatively little seasonality (Isbell et al., 2017), we believe that results from our data collection period are generalizable to other months.

We explicitly considered and analyzed the influence of life stage, as well as the influence of the lunar cycle, on sleep patterns.

(vi) Genetic make-up

We have no reason to suspect that the genetic make-up of the study individuals would bias their sleep patterns in comparison to other populations of olive baboons.

(vii) Experience

All study individuals experienced trapping and collaring procedures for the first time during this study, and thus, were equally naïve. See "Acclimation and habituation" for discussion of the potential for experience with humans during collaring procedures to influence sleep patterns.

Acknowledgments

We are grateful to the Kenya National Science and Technology Council (NCTS/RCD/12B/012/26B, NACOSTI/P/15/5727/4608, NACOSTI/P/19/55517/24299, NACOSTI/P/20/1407), Kenyan Wildlife Service (KWS/BRM/5001), and Mpala Research Centre for permission to conduct research. Research procedures received IACUC approval (Smithsonian Tropical Research Institute, assurance number 2012.0601.2015; University of California, Davis, assurance number 20442). We thank Ariana Strandburg-Peshkin, Alison Ashbury, and Niels Rattenborg for helpful comments on previous drafts of the manuscript. We thank M Wikelski, E Bermingham, D Rubenstein, M Kinnaird, D Carlino, Y Dellenback, S Dyer and B Tripard for logistical support, as well as R Kays, S Murray, M Mutinda, R Lessnau, S Alavi, J Nairobi, F Kuemmeth, and W Heidrich for field assistance. We are grateful to Shauhin Alavi for his statistical advice throughout the analysis. We thank Yuuki Watanabe and an anonymous reviewer for providing productive comments and suggestions on the submitted manuscript that greatly improved the quality of the manuscript. This research received funding from the Max Planck Institute for Ornithology, the Smithsonian Tropical Research Institute, and University of California, Davis. RH and MCC were supported by the National Science Foundation (IIS 1514174 & IOS 1250895). MCC received additional support from a Packard Foundation Fellowship (2016-65130), and the Alexander von Humboldt Foundation in the framework of the Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research. JCL was supported by a National Science

Foundation Graduate Research Fellowship, the National Science Foundation Graduate Research Internship Program, a Dean's Distinguished Graduate Fellowship from the University of California, Davis, and a Richard G. Coss Wildlife Research Fellowship. Further support for the project was also provided by the Center for the Advanced Study of Collective Behavior at the University of Konstanz, Deutsche Forschungsgemeinschaft Centre of Excellence 2117 (ID: 422037984).

Data availability

GPS and accelerometry data generated during this study are published and available in the Movebank repository (www.movebank.org; Crofoot et al. 2021). Drone imagery is publicly available for download from Dryad (http://dx.doi.org/10.5061/dryad.6h5b7). Accelerometry data and behavioral scoring data from the 2019 sleep validation study are also publicly available for download from Dryad (https://doi.org/10.5061/dryad.p5hqbzkqf). All code used to produce the final results from the raw data is on GitHub (https://github.com/CarterLoftus/baboon_sleep/) and archived on Zenodo (https://doi.org/10.5281/zenodo.5905742).

Supplemental Materials

Sleep validation study

To evaluate whether the accelerometer-based sleep classification technique was accurately monitoring sleep in baboons, we returned to Mpala Research Centre in July 2019 to perform a validation study in which we compared the results of the accelerometer-based sleep classification to direct observations of awake and sleeping baboons. Using the procedures described in Strandburg-Peshkin et al., 2015, we trapped and anesthetized 27 members of a group of habituated olive baboons, fitting each with a GPS and accelerometry collar. Eleven of the 27 collars deployed recorded continuous tri-axial accelerations at 12 Hz/axis from 06:30 to 18:00 and 0.71-second bursts of accelerations at 56.2 Hz/axis at the beginning of every minute from 18:00 to 06:30. Accelerometry data was collected by each of these 11 collars for up to 31 days. The remaining 16 collars did not collect accelerometry data from 06:30 to 18:00, and thus we excluded data from these collars from the validation study.

We down-sampled and interpolated the accelerometry data such that it matched the sampling frequency and schedule of the data collected in 2012 (i.e. the data analyzed for this manuscript). We

then applied the sleep classification algorithm described in the Materials and Methods to this validation dataset.

To validate the sleep classification algorithm, we performed direct behavioral observations of the baboons at their primary sleep site. We recorded the behavior of the study baboons starting when they approached their sleep site using a FLIR T1020 high-resolution infrared camera (FLIR Systems Inc., Wilsonville, OR, USA). Recordings continued into the night for as long as the camera battery allowed (average recording duration [range of recording durations]: 7.4 hours [1.7 – 14.9 hours]), and we collected infrared imaging data on 21 nights. We identified individuals in the infrared imagery both in real-time, via observer narration of the recorded imagery, and post-recording, by matching movements of individuals in the infrared imagery to the GPS tracks of collared individuals.

Following initial data collection, we used the commercial software Loopy (Loopbio GmbH, Austria) to score the behavior of identified individuals in the infrared imagery. Individuals' behavior was scored as "wakefulness", "resting wakefulness", or "sleep" (Figure 1.5-figure supplement 1). Wakefulness refers to any behavior involving active movement (i.e. walking, running) or engaged activity (i.e. allogrooming), whereas resting wakefulness refers to behaviors that are dormant (i.e. sitting), but not in the typical sleeping posture of a baboon (sitting or lying with neck relaxed and head hung). Sustained dormant behavior in the typical sleep posture was considered sleep. Video scoring resulted in a total of 8.0 hours of behavioral observation across a total of 16 individual baboons.

Synchronizing the infrared imagery data with the accelerometry data produced a validation dataset of 301 minute-epochs across six baboons that were both classified as either sleep or wakeful behavior from accelerometry, and scored as wakefulness, resting wakefulness, or sleep from direct observation. With both wakefulness and resting wakefulness representing wakeful behavior, the accelerometer-based sleep classification exhibited an accuracy of 80.7% (Supplementary file 1r). Consistent with previous validation studies of the use of accelerometry in measuring sleep (Ancoli-Israel et al., 2003; de Souza et al., 2003), we found that accelerometer-based sleep classification has difficulty distinguishing resting wakefulness from sleep, and we consider this limitation in our interpretation of the results.

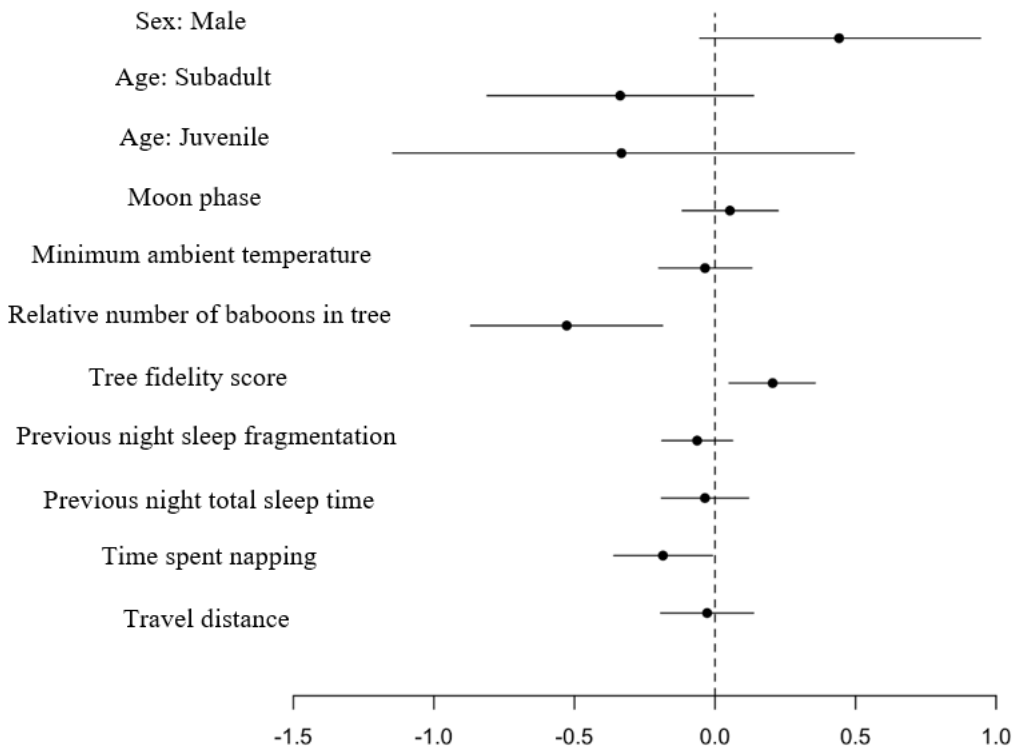

Figure 1.2-figure supplement 1. Model output plot of model of total sleep time (for the first 20 days) with all numerical variables standardized. The categorical variable tree is not plotted.

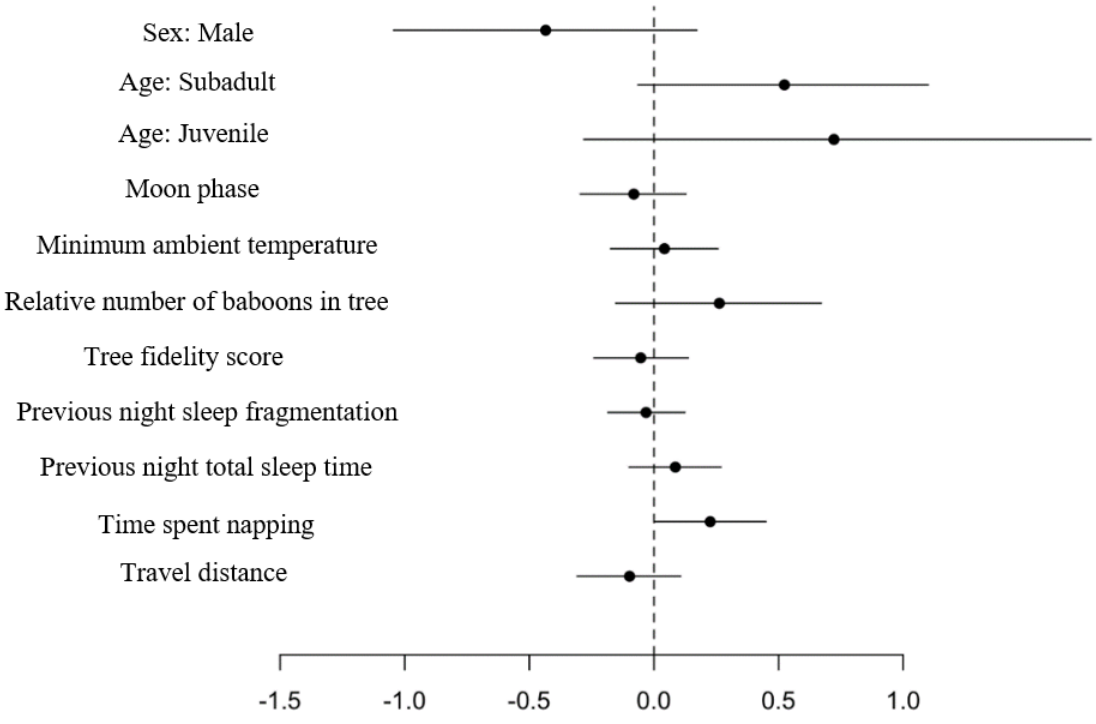

Figure 1.2-figure supplement 2. Model output plot of model of sleep fragmentation (for the first 20 days) with all numerical variables standardized. The categorical variable tree is not plotted.

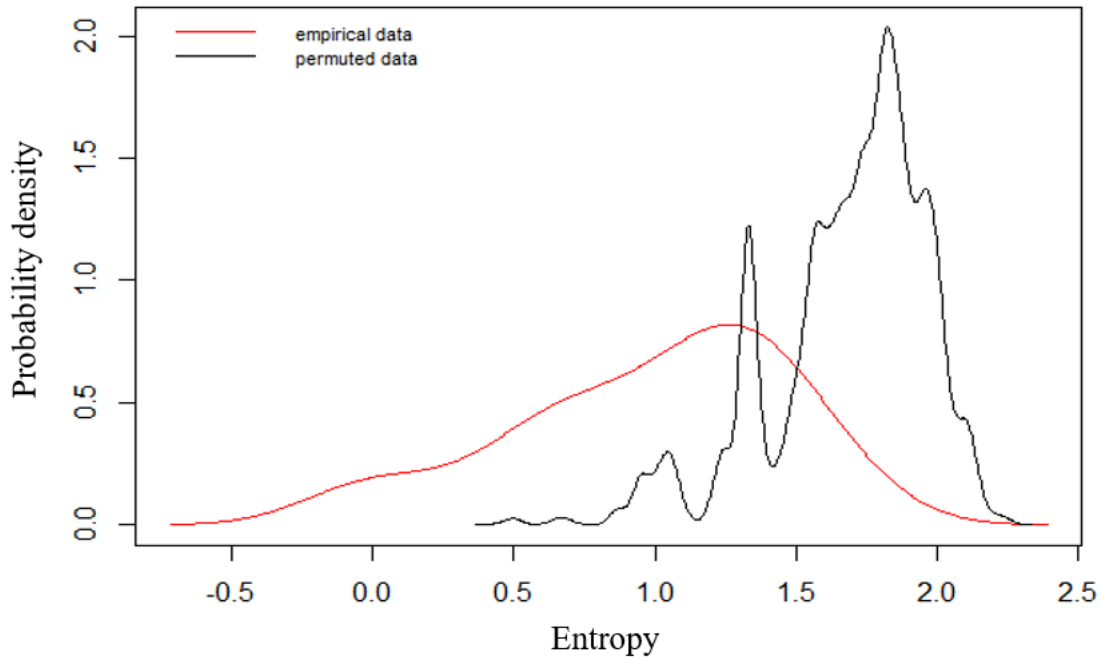

Figure 1.3-figure supplement 1. Comparison of the Shannon entropies of individuals' sleep tree occupancy within this sleep site to a null distribution produced by 1000 identity permutations. The analysis revealed lower entropy in tree occupancy than expected by random chance (one-tailed two-sample Kolmogorov-Smirnov test: $p < 1.0 \times 10^{-9}$), indicating that individuals exhibited high fidelity to particular trees. The red line represents the distribution of Shannon entropies of individuals' sleep tree occupancy calculated from the empirical data, and the black line represents the distribution of entropy of sleep tree occupancy derived from the permuted data set.

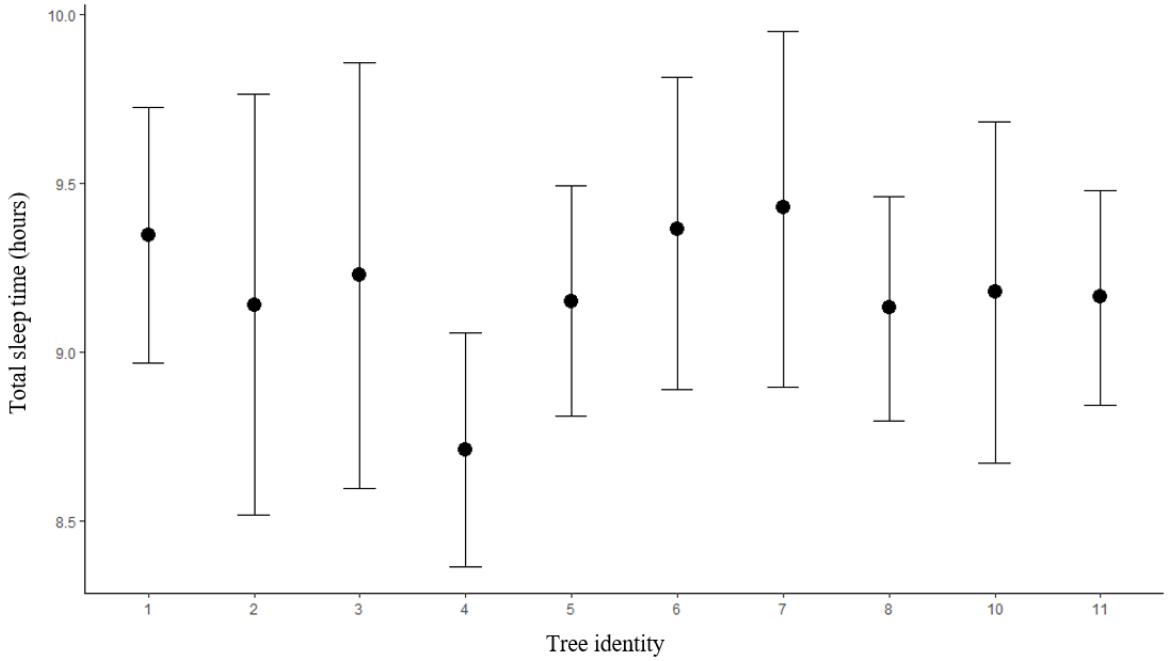

Figure 1.3-figure supplement 2. The conditional effect of tree identity on total sleep time. The conditional effects plotted here are from the unstandardized Bayesian linear mixed model (LMM) of total sleep time (hours).

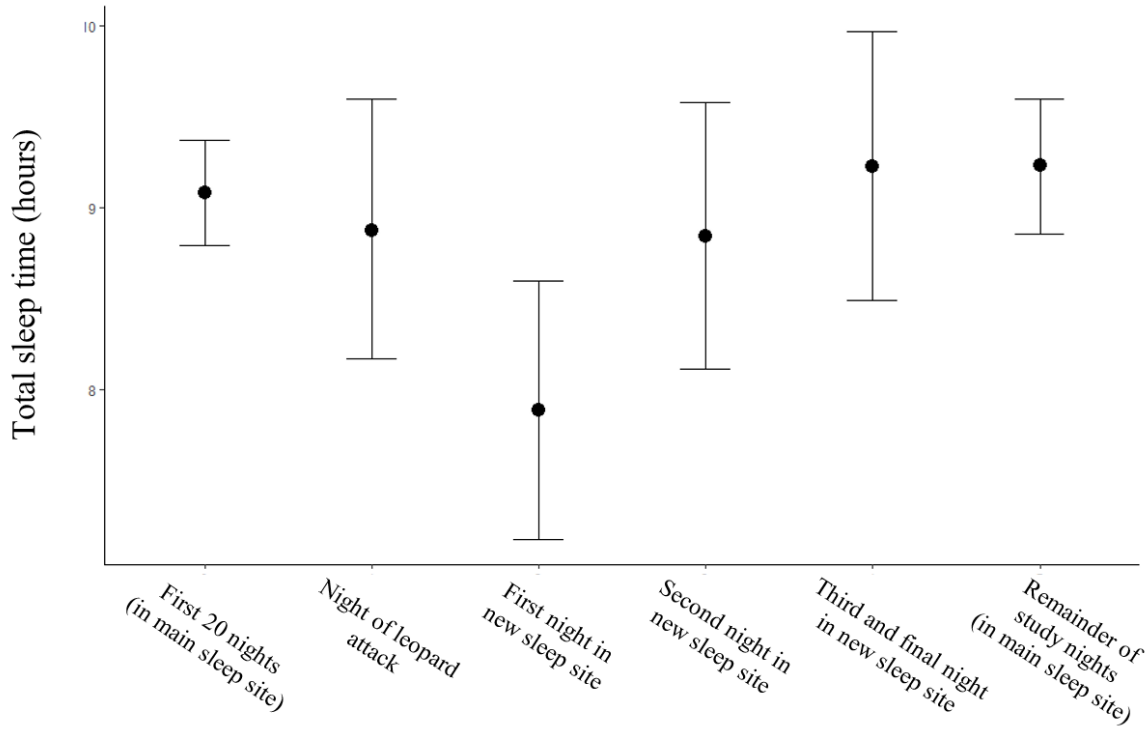

Figure 1.3-figure supplement 3. The conditional effect of night condition on total sleep time. The conditional effects presented here are from the unstandardized model of total sleep time.

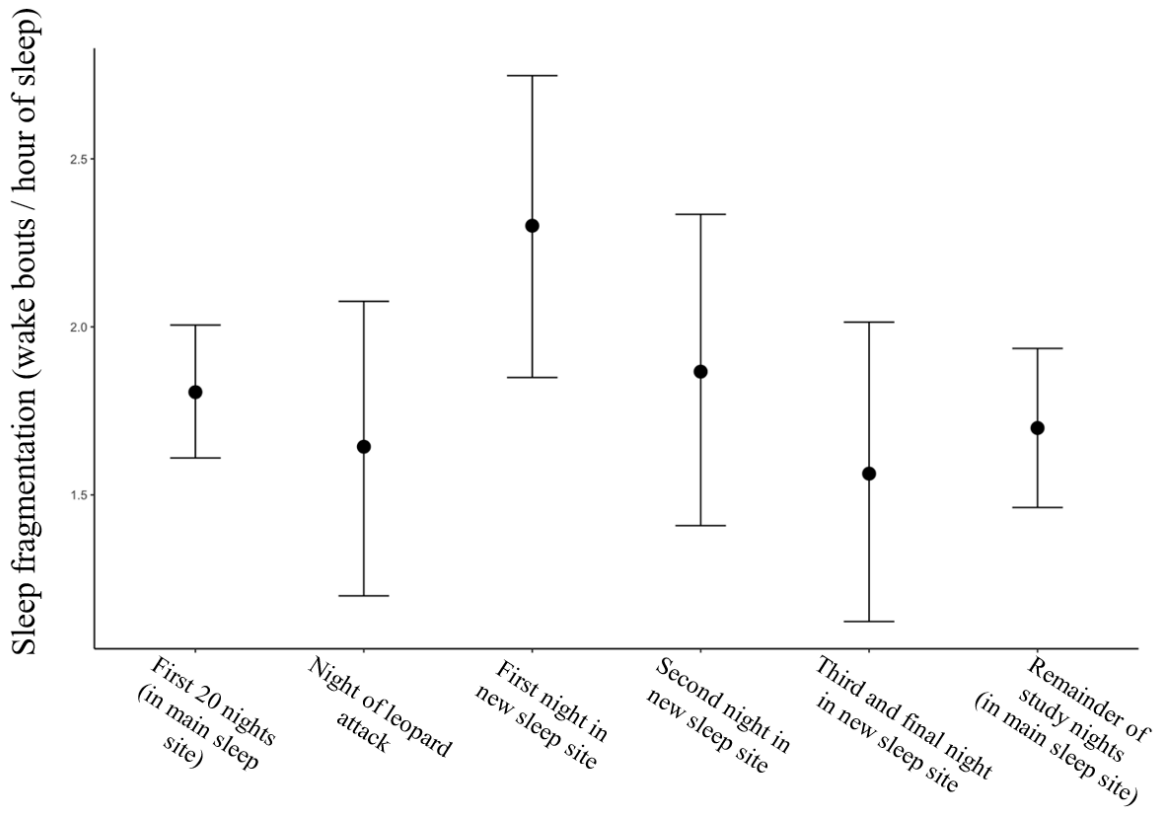

Figure 1.3-figure supplement 4. The conditional effect of night condition on sleep fragmentation. The conditional effects presented here are from the unstandardized model of sleep fragmentation.

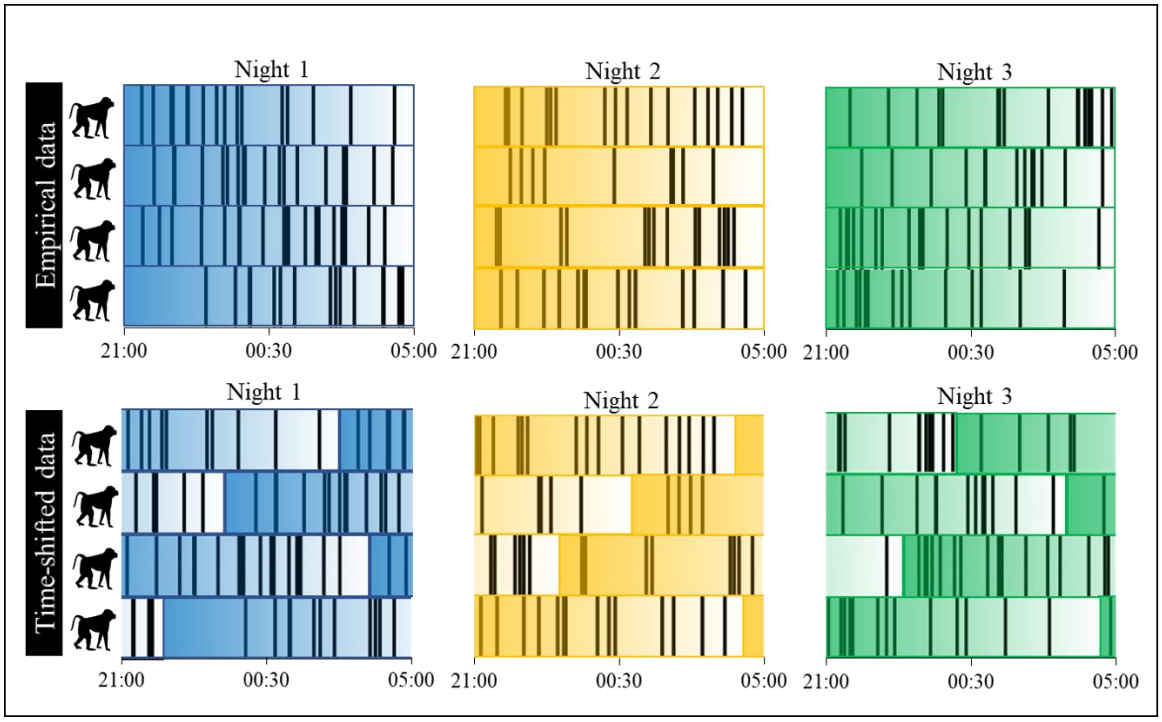

Figure 1.4-figure supplement 1. A toy example of the procedure we used to test for sentinel behavior and synchronization of nighttime behavior. Each row represents a baboon's time-series of sleep and wake activity during the night, with black vertical lines indicating periods of nocturnal waking behavior. Colors correspond to different nights, and the transparency of the color indicates the timing of night, with reference to the empirical, unshifted data. The time shifting procedure was repeated 1000 times to generate a null distribution for the proportion of minutes in which at least one individual is awake during the night and the mean proportion of the group exhibiting synchronized behavior.

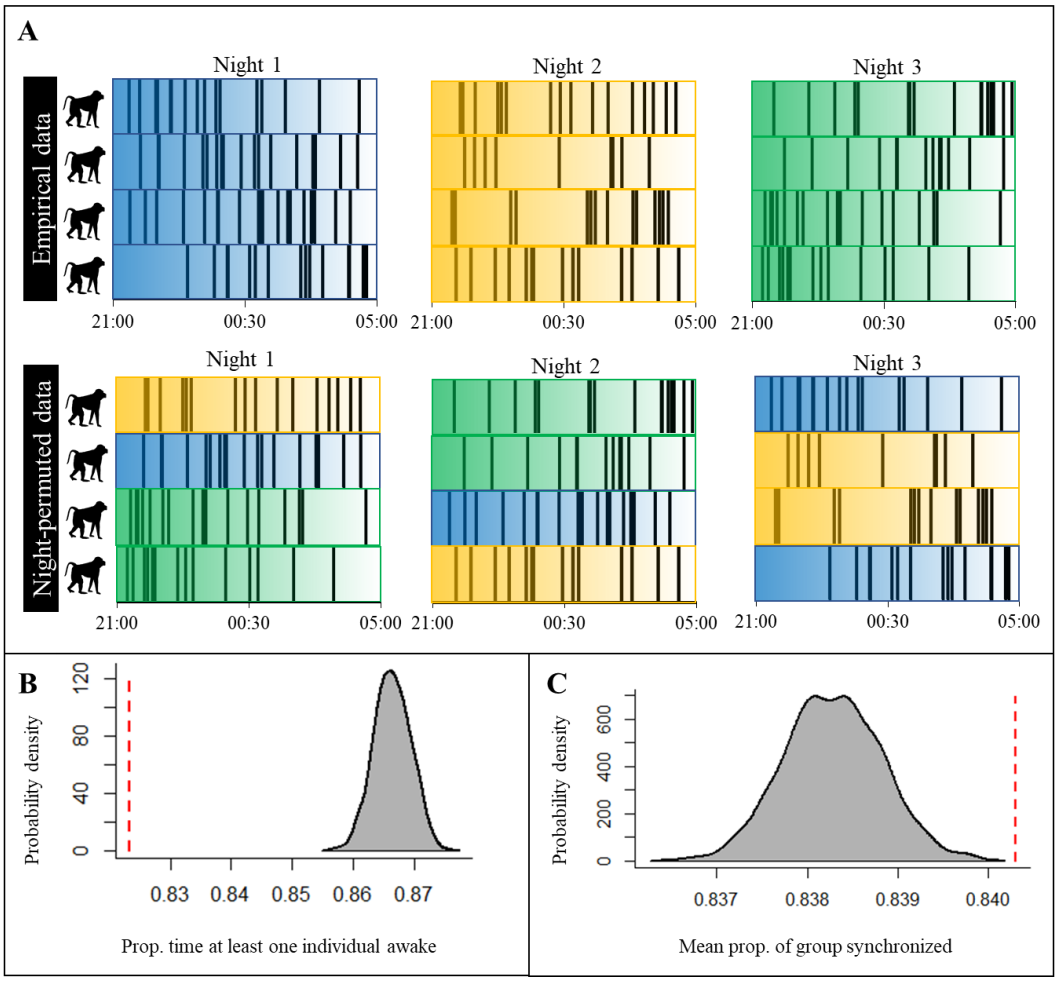

Figure 1.4-figure supplement 2. A) A toy example of the procedure alternative to the one presented in the main text (and represented in Figure 1.4-figure supplement 1) that we used to confirm findings concerning sentinel behavior and synchronization of nighttime behavior that we derived from the procedure presented in the main text. Each row represents a baboon's time-series of sleep and wake activity during the night, with black vertical lines indicating periods of nocturnal waking behavior. Colors correspond to different nights, with reference to the empirical, unpermuted data, and the transparency of the color indicates the timing of night. The night permutation procedure was repeated 1000 times to generate a null distribution for the proportion of minutes in which at least one individual is awake during the night and the mean proportion of the group exhibiting synchronized behavior. B) Comparison of the empirical proportion of minutes in which at least one individual is awake (red dotted line) to its null distribution (grey density plot; $p < 0.0001$). C) Comparison of the empirical mean of the proportion of the group exhibiting synchronized behavior (red dotted line) to its null distribution (grey density plot; $p < 0.0001$). This method of permutation controls for the possibility that baboons are synchronized in their behavior simply as a result of species-typical nocturnal waking patterns that are consistent across baboons and across nights.

Figure 1.5-figure supplement 1. Examples of the three different behaviors, “wakefulness”, “resting wakefulness”, and “sleep”, that were scored during the validation study. Images presented here are extracted from the infrared imaging that was used for the behavioral scoring.

Collar #	Sex	Age	Weight (kg)	Capture date	GPS/ACC start date	GPS end date	ACC end date
2460	F	A	12	2012-07-28	2012-08-01	2012-08-01	2012-08-01
2459	F	SA	8.6	2012-07-22	2012-08-01	2012-08-01	2012-08-01
2458	F	A	13	2012-07-22	2012-08-01	2012-08-01	2012-08-01
2457	M	A	28	2012-07-21	2012-08-01	2012-09-04	2012-09-04
2456	F	A	17.5	2012-07-22	2012-08-01	2012-08-31	2012-08-31
2455	F	SA	10	2012-07-28	2012-08-01	2012-08-08	2012-08-08
2454	M	J	9.25	2012-07-22	2012-08-01	2012-08-14	2012-08-14
2453	F	A	11.2	2012-07-25	2012-08-01	2012-08-03	2012-08-03
2452	M	SA	9	2012-07-21	2012-08-01	2012-08-14	2012-08-14
2451	F	A	13	2012-07-22	2012-08-01	2012-09-02	2012-09-02
2450	F	SA	8.85	2012-07-24	2012-08-01	2012-08-05	2012-08-05
2449	F	A	12.75	2012-07-23	2012-08-01	2012-08-31	2012-08-31
2448	M	J	6.65	2012-07-22	2012-08-01	2012-08-16	2012-08-17
2447	F	A	12.25	2012-07-24	2012-08-01	2012-08-31	2012-08-31
2446	F	A	15.75	2012-07-25	2012-08-01	2012-09-02	2012-09-02
2443	M	SA	9.25	2012-07-23	2012-08-01	2012-09-02	2012-09-02
2441	F	SA	8	2012-07-22	2012-08-01	2012-08-29	2012-08-29
2439	F	A	16	2012-07-21	2012-08-01	2012-09-04	2012-09-04
2436	M	SA	16	2012-07-22	2012-08-01	2012-09-02	2012-09-02
2434	M	A	25	2012-07-22	2012-08-01	2012-08-02	2012-08-02
2433	M	SA	10	2012-07-22	2012-08-01	2012-08-06	2012-08-06
2432	M	SA	8	2012-07-22	2012-08-01	2012-08-05	2012-08-05
2430	F	A	14.65	2012-07-28	2012-08-01	2012-08-03	2012-08-03
2428	F	SA	8.5	2012-07-29	2012-08-01	2012-08-15	2012-08-15

2427	M	A	25	2012-07-21	2012-08-01	2012-09-04	2012-09-04
2426	M	SA	20	2012-07-21	2012-08-01	2012-08-30	2012-08-31

Supplementary file 1a. Individual metadata. Table depicts the sex, age, weight, capture date, as well as data collection start and end dates for each study individual. F = female, M = male, A = adult, SA = subadult, J = juvenile, ACC = accelerometry.

	Total sleep time	Sleep onset time	Waking time	Sleep period duration	Sleep efficiency	Sleep fragmentation
Total sleep time	1	-0.61	0.65	0.87	0.57	-0.48
Sleep onset time	x	1	-0.04	-0.72	-0.05	0.03
Waking time	x	x	1	0.72	0.10	-0.10
Sleep period duration	x	x	x	1	0.11	-0.09
Sleep efficiency	x	x	x	x	1	-0.83
Sleep Fragmentation	x	x	x	x	x	1

Supplementary file 1b. Pearson correlation coefficient between the metrics of sleep extracted from the accelerometry data. Total sleep time is correlated with all sleep metrics.

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.02	-0.50 – 0.53
Travel distance	-0.03	-0.19 – 0.14
Time spent napping	-0.19	-0.36 – -0.01
Previous night relative total sleep time	-0.04	-0.19 – 0.12
Previous night relative sleep fragmentation	-0.06	-0.19 – 0.06
Tree fidelity score	0.21	0.05 – 0.36
Relative number of baboons in tree	-0.53	-0.87 – -0.19
Minimum ambient temperature	-0.04	-0.20 – 0.13
Moon phase	0.05	-0.12 – 0.22
age: Juvenile	-0.34	-1.15 – 0.50
age: Subadult	-0.34	-0.81 – 0.14
sex: Male	0.44	-0.05 – 0.94
tree: tree2	-0.26	-1.08 – 0.55
tree: tree3	-0.19	-1.06 – 0.66
tree: tree4	-0.85	-1.35 – -0.33
tree: tree5	-0.27	-0.79 – 0.24
tree: tree6	-0.02	-0.66 – 0.63
tree: tree7	0.05	-0.68 – 0.79
tree: tree8	-0.28	-0.77 – 0.20
tree: tree10	-0.29	-1.04 – 0.47
tree: tree11	-0.26	-0.84 – 0.30

Random Effects	
σ^2	0.53
$\tau_{00\ night}$	0.02
$\tau_{00\ tag}$	0.09
ICC	0.17
N_{tag}	18
N_{night}	18
Observations	170
Marginal R^2 / Conditional R^2	0.345 / 0.419

Supplementary file 1c. Model output table of model of total sleep time (for the first 20 days) with all numerical variables standardized.

	Total sleep time (hours)	
Predictors	*Estimates*	*CI (95%)*
Intercept	19.09	-24.89 – 63.56
Travel distance (km)	-0.02	-0.12 – 0.09
Time spent napping (mins)	-0.01	-0.01 – -0.00
Previous night relative total sleep time (mins)	-0.00	-0.00 – 0.00
Previous night relative sleep fragmentation (bouts/hour of sleep)	-0.11	-0.33 – 0.11
Tree fidelity score	0.61	0.16 – 1.08
Relative number of baboons in tree	-1.61	-2.67 – -0.52
Minimum ambient temperature (degree Celsius)	-0.03	-0.19 – 0.12
Moon phase	0.11	-0.24 – 0.50
age: Juvenile	-0.27	-0.88 – 0.36
age: Subadult	-0.27	-0.63 – 0.08
sex: Male	0.34	-0.02 – 0.72
tree: tree2	-0.20	-0.82 – 0.45
tree: tree3	-0.14	-0.81 – 0.52
tree: tree4	-0.66	-1.04 – -0.26
tree: tree5	-0.22	-0.61 – 0.18
tree: tree6	-0.01	-0.50 – 0.49
tree: tree7	0.05	-0.52 – 0.63
tree: tree8	-0.23	-0.60 – 0.15
tree: tree10	-0.21	-0.80 – 0.37
tree: tree11	-0.21	-0.66 – 0.22
Random Effects		
σ^2	0.31	
$\tau_{00\ night}$	0.01	
$\tau_{00\ tag}$	0.05	
ICC	0.17	
N_{tag}	18	
N_{night}	18	
Observations	170	
Marginal R^2 / Conditional R^2	0.342 / 0.417	

Supplementary file 1d. Model output table of model of total sleep time (for the first 20 days) with no standardization of variables.

	Total sleep time (standardized)

Predictors	*Estimates*	*CI (95%)*
Intercept	0.01	-0.51 – 0.51
Average VeDBA during day	-0.12	-0.34 – 0.12
Time spent napping	-0.13	-0.31 – 0.05
Previous night relative total sleep time	-0.04	-0.18 – 0.11
Previous night relative sleep fragmentation	-0.08	-0.20 – 0.05
Tree fidelity score	0.21	0.05 – 0.36
Relative number of baboons in tree	-0.57	-0.91 – -0.21
Minimum ambient temperature	-0.04	-0.21 – 0.12
Moon phase	0.07	-0.09 – 0.24
age: Juvenile	-0.23	-1.03 – 0.55
age: Subadult	-0.27	-0.78 – 0.18
sex: Male	0.53	0.08 – 0.97
tree: tree2	-0.33	-1.15 – 0.49
tree: tree3	-0.51	-1.30 – 0.29
tree: tree4	-0.89	-1.41 – -0.37
tree: tree5	-0.31	-0.83 – 0.21
tree: tree6	0.00	-0.63 – 0.62
tree: tree7	0.05	-0.69 – 0.79
tree: tree8	-0.30	-0.79 – 0.20
tree: tree10	-0.18	-0.90 – 0.55
tree: tree11	-0.28	-0.84 – 0.28
Random Effects		
σ^2	0.55	
$\tau_{00\ night}$	0.02	
$\tau_{00\ tag}$	0.07	
ICC	0.13	
N_{tag}	18	
N_{night}	18	
Observations	178	
Marginal R^2 / Conditional R^2	0.358 / 0.419	

Supplementary file 1e. Model output table of model of total sleep time (for the first 20 days) with all numerical variables standardized (daytime VeDBA included instead of travel distance).

	Time spent napping (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.05	-0.44 – 0.33
Prior night total sleep time	0.03	-0.10 – 0.17
Prior night sleep fragmentation	0.00	-0.11 – 0.12
Random Effects		
σ^2	0.42	
$\tau_{00\ night}$	0.21	
$\tau_{00\ tag}$	0.44	
ICC	0.61	
N_{tag}	20	
N_{night}	19	
Observations	202	
Marginal R^2 / Conditional R^2	0.005 / 0.616	

Supplementary file 1f. Model output table of model of time spent napping during the day (for the first 20 days) with all numerical variables standardized.

	Time spent napping (minutes)	
Predictors	*Estimates*	*CI (95%)*
Intercept	17.52	-9.03 – 45.26
Prior night total sleep time (hours)	1.16	-1.62 – 3.86
Prior night sleep fragmentation (bouts/hour of sleep)	0.12	-2.87 – 3.21
Random Effects		
σ^2	226.61	
$\tau_{00\ night}$	40.73	
$\tau_{00\ tag}$	78.33	
ICC	0.34	
N_{tag}	20	
N_{night}	19	
Observations	202	
Marginal R^2 / Conditional R^2	0.003 / 0.536	

Supplementary file 1g. Model output table of model of time spent napping during the day (for the first 20 days) without standardization of the variables.

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.25	-0.60 – 0.09
cond_night: night of leopard encounter	-0.20	-0.85 – 0.45
cond_night: first night in new sleep site	-1.52	-2.15 – -0.86
cond_night: second night in new sleep site	-0.29	-0.98 – 0.42
cond_night: third night in new sleep site	0.24	-0.45 – 0.90
cond_night: remainder of nights (in original sleep site)	0.27	-0.05 – 0.58
age: Juvenile	-0.24	-1.10 – 0.61
age: Subadult	-0.35	-0.86 – 0.16
sex: Male	0.75	0.22 – 1.30
Travel distance	-0.06	-0.18 – 0.07
Time spent napping	-0.12	-0.28 – 0.05
Previous night relative total sleep time	0.18	0.06 – 0.29
Previous night relative sleep fragmentation	0.06	-0.06 – 0.19
Minimum ambient temperature	-0.01	-0.15 – 0.14
Moon phase	0.02	-0.12 – 0.16
Random Effects		
σ^2	0.78	
$\tau_{00\ tag}$	0.15	
ICC	0.16	
N_{tag}	20	
Observations	275	
Marginal R^2 / Conditional R^2	0.253 / 0.318	

Supplementary file 1h. Model output table of model of total sleep time using data from entire study duration (including after the leopard encounter) with all variables standardized.

	Total sleep time (hours)	
Predictors	*Estimates*	*CI (95%)*
Intercept	10.50	-42.03 – 61.10
cond_night: night of leopard encounter	-0.17	-0.88 – 0.53
cond_night: first night in new sleep site	-1.17	-1.87 – -0.47
cond_night: second night in new sleep site	-0.24	-0.97 – 0.49
cond_night: third night in new sleep site	0.15	-0.57 – 0.89
cond_night: remainder of nights (in original sleep site)	0.17	-0.17 – 0.49
age: Juvenile	-0.27	-0.96 – 0.41
age: Subadult	-0.31	-0.72 – 0.08
sex: Male	0.59	0.19 – 1.01
Travel distance (km)	-0.04	-0.14 – 0.05
Time spent napping (mins)	-0.00	-0.01 – 0.00
Previous night relative total sleep time (mins)	0.00	0.00 – 0.01
Previous night relative sleep fragmentation (bouts/hour of sleep)	0.12	-0.10 – 0.33
Minimum ambient temperature (degrees Celsius)	-0.00	-0.18 – 0.18
Moon phase	0.07	-0.34 – 0.48
Random Effects		
σ^2	0.43	
$\tau_{00\ night}$	0.05	
$\tau_{00\ tag}$	0.09	
ICC	0.25	
N_{tag}	20	
N_{night}	32	
Observations	275	
Marginal R^2 / Conditional R^2	0.262 / 0.369	

Supplementary file 1i. Model output table of model of total sleep time using data from entire study duration (including after the leopard encounter) without standardization of variables.

	Sleep fragmentation (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.27	-0.93 – 0.37
Travel distance	-0.10	-0.31 – 0.11
Time spent napping	0.22	0.00 – 0.45
Previous night relative total sleep time	0.09	-0.10 – 0.27
Previous night relative sleep fragmentation	-0.03	-0.18 – 0.12
Tree fidelity score	-0.05	-0.24 – 0.14
Relative number of baboons in tree	0.26	-0.15 – 0.67
Minimum ambient temperature	0.04	-0.17 – 0.26
Moon phase	-0.08	-0.30 – 0.13
age: Juvenile	0.72	-0.28 – 1.75
age: Subadult	0.52	-0.06 – 1.10
sex: Male	-0.44	-1.04 – 0.17
tree: tree2	0.91	-0.08 – 1.89
tree: tree3	0.37	-0.67 – 1.39
tree: tree4	0.60	-0.03 – 1.20

tree: tree5	0.69	0.07 – 1.30
tree: tree6	0.54	-0.26 – 1.30
tree: tree7	-0.22	-1.14 – 0.69
tree: tree8	-0.04	-0.64 – 0.55
tree: tree10	-0.00	-0.90 – 0.90
tree: tree11	0.48	-0.21 – 1.15
Random Effects		
σ^2	0.79	
$\tau_{00\ night}$	0.04	
$\tau_{00\ tag}$	0.14	
ICC	0.19	
N_{tag}	18	
N_{night}	18	
Observations	170	
Marginal R^2 / Conditional R^2	0.266 / 0.352	

Supplementary file 1j. Model output table of model of sleep fragmentation (for the first 20 days) with all numerical variables standardize.

	Sleep fragmentation (wake bouts / hour of sleep)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-5.74	-44.05 – 31.71
Travel distance (km)	-0.04	-0.13 – 0.05
Time spent napping (mins)	0.01	0.00 – 0.01
Previous night relative total sleep time (mins)	0.00	-0.00 – 0.00
Previous night relative sleep fragmentation (bouts/hour of sleep)	-0.04	-0.21 – 0.15
Tree fidelity score	-0.10	-0.47 – 0.26
Relative number of baboons in tree	0.55	-0.33 – 1.45
Minimum ambient temperature (degree Celsius)	0.03	-0.10 – 0.16
Moon phase	-0.12	-0.43 – 0.18
age: Juvenile	0.38	-0.14 – 0.91
age: Subadult	0.28	-0.02 – 0.57
sex: Male	-0.23	-0.55 – 0.08
tree: tree2	0.50	-0.03 – 1.01
tree: tree3	0.22	-0.34 – 0.77
tree: tree4	0.33	-0.00 – 0.66
tree: tree5	0.37	0.04 – 0.72
tree: tree6	0.29	-0.12 – 0.71
tree: tree7	-0.10	-0.58 – 0.40
tree: tree8	0.00	-0.31 – 0.32
tree: tree10	0.02	-0.47 – 0.51
tree: tree11	0.27	-0.10 – 0.64
Random Effects		
σ^2	-0.04	
$\tau_{00\ night}$	0.01	
$\tau_{00\ tag}$	0.00	
ICC	-0.04	
N_{tag}	-0.10	
N_{night}	0.55	

Observations	0.03
Marginal R^2 / Conditional R^2	-0.12

Supplementary file 1k. Model output table of model of sleep fragmentation (for the first 20 days) with no standardization of variables.

	Sleep fragmentation (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.29	-0.95 – 0.34
Average VeDBA during day	-0.05	-0.33 – 0.23
Time spent napping	0.20	-0.02 – 0.42
Previous night relative total sleep time	0.07	-0.11 – 0.25
Previous night relative sleep fragmentation	-0.03	-0.19 – 0.12
Tree fidelity score	-0.06	-0.25 – 0.13
Relative number of baboons in tree	0.24	-0.18 – 0.65
Minimum ambient temperature	0.07	-0.14 – 0.27
Moon phase	-0.10	-0.30 – 0.11
age: Juvenile	0.75	-0.25 – 1.76
age: Subadult	0.62	-0.00 – 1.24
sex: Male	-0.46	-1.04 – 0.12
tree: tree2	0.85	-0.13 – 1.82
tree: tree3	0.45	-0.51 – 1.40
tree: tree4	0.55	-0.07 – 1.17
tree: tree5	0.65	0.03 – 1.28
tree: tree6	0.43	-0.34 – 1.22
tree: tree7	-0.21	-1.08 – 0.70
tree: tree8	-0.05	-0.64 – 0.56
tree: tree10	0.09	-0.79 – 0.97
tree: tree11	0.38	-0.28 – 1.06
Random Effects		
σ^2	0.80	
$\tau_{00\ night}$	0.03	
$\tau_{00\ tag}$	0.14	
ICC	0.17	
N_{tag}	18	
N_{night}	18	
Observations	178	
Marginal R^2 / Conditional R^2	-0.29	

Supplementary file 1l. Model output table of model of sleep fragmentation (for the first 20 days) with all numerical variables standardized (daytime VeDBA included instead of travel distance).

	Sleep fragmentation (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.05	-0.33 – 0.44
cond_night: night of leopard encounter	-0.32	-0.96 – 0.33
cond_night: first night in new sleep site	0.96	0.33 – 1.60
cond_night: second night in new sleep site	0.10	-0.60 – 0.80
cond_night: third night in new sleep site	-0.48	-1.16 – 0.20

cond_night: remainder of nights (in original sleep site)	-0.20	-0.52 – 0.11
age: Juvenile	0.69	-0.26 – 1.60
age: Subadult	0.48	-0.09 – 1.03
sex: Male	-0.53	-1.10 – 0.05
Travel distance	0.01	-0.12 – 0.13
Time spent napping	0.21	0.05 – 0.38
Previous night relative total sleep time	0.02	-0.10 – 0.14
Previous night relative sleep fragmentation	-0.08	-0.20 – 0.04
Minimum ambient temperature	0.10	-0.04 – 0.24
Moon phase	-0.05	-0.18 – 0.09
Random Effects		
σ^2	0.79	
$\tau_{00\ tag}$	0.20	
ICC	0.20	
N_{tag}	20	
Observations	275	
Marginal R^2 / Conditional R^2	0.175 / 0.298	

Supplementary file 1m. Model output table of model of sleep fragmentation using data from entire study duration (including after the presumed leopard encounter) with all variables standardized.

	Sleep fragmentation (wake bouts / hour of sleep)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-15.99	-47.39 – 14.91
cond_night: night of leopard encounter	-0.16	-0.58 – 0.24
cond_night: first night in new sleep site	0.50	0.07 – 0.92
cond_night: second night in new sleep site	0.06	-0.38 – 0.51
cond_night: third night in new sleep site	-0.24	-0.67 – 0.19
cond_night: remainder of nights (in original sleep site)	-0.11	-0.31 – 0.10
age: Juvenile	0.37	-0.11 – 0.85
age: Subadult	0.25	-0.05 – 0.53
sex: Male	-0.27	-0.55 – 0.02
Travel distance (km)	0.00	-0.06 – 0.06
Time spent napping (mins)	0.00	0.00 – 0.01
Previous night relative total sleep time (mins)	0.00	-0.00 – 0.00
Previous night relative sleep fragmentation (bouts/hour of sleep)	-0.09	-0.23 – 0.05
Minimum ambient temperature (degrees Celsius)	0.06	-0.05 – 0.17
Moon phase	-0.06	-0.30 – 0.19
Random Effects		
σ^2	0.19	
$\tau_{00\ night}$	0.01	
$\tau_{00\ tag}$	0.05	
ICC	0.24	
N_{tag}	20	
N_{night}	32	
Observations	275	
Marginal R^2 / Conditional R^2	0.185 / 0.329	

Supplementary file 1n. Model output table of model of sleep fragmentation using data from entire study duration (including after the presumed leopard encounter) without standardization of variables.

	Proportion of minutes synchronized (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.21	-0.45 – 0.03
Occupying same tree	0.56	0.47 – 0.64
Random Effects		
σ^2	0.60	
$\tau_{00\ dy\_name}$	0.14	
$\tau_{00\ night}$	0.19	
$\tau_{00\ tag1}$	0.08	
$\tau_{00\ tag2}$	0.09	
ICC	0.45	
N_{night}	34	
N_{tag1}	22	
N_{tag2}	22	
N_{dy_name}	250	
Observations	2997	
Marginal R^2 / Conditional R^2	0.050 / 0.404	

Supplementary file 1o. Model output table of model of synchronization (i.e. the proportion of minutes during a night that both dyad members exhibit the same behavior, either sleep or wakefulness) with response variable standardized of the response variable.

	Proportion of minutes synchronized	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.73	0.71 – 0.74
Occupying same tree	0.03	0.02 – 0.03
Random Effects		
σ^2	0.00	
$\tau_{00\ dy\_name}$	0.00	
$\tau_{00\ night}$	0.00	
$\tau_{00\ tag1}$	0.00	
$\tau_{00\ tag2}$	0.00	
ICC	0.45	
N_{night}	34	
N_{tag1}	22	
N_{tag2}	22	
N_{dy_name}	250	
Observations	2997	
Marginal R^2 / Conditional R^2	0.050 / 0.404	

Supplementary file 1p. Model output table of model of synchronization (i.e. the proportion of minutes during a night that both dyad members exhibit the same behavior, either sleep or wakefulness) without standardization of the response variable.

	Focal baboon awake in the current epoch	
Predictors	*Odds Ratios*	*CI (95%)*
Intercept	0.07	0.07 – 0.08
At least one group-mate in the same sleep tree awake in previous epoch	1.29	1.18 – 1.40
Previous night relative total sleep time	1.04	0.98 – 1.11
Previous night relative sleep fragmentation	1.01	0.96 – 1.06
At least one neighbor awake x previous night relative total sleep time	0.99	0.88 – 1.11
At least one neighbor awake x previous night relative sleep fragmentation	0.99	0.90 – 1.09
Random Effects		
σ^2	3.29	
$\tau_{00\ night}$	0.01	
$\tau_{00\ tag}$	0.01	
ICC	0.00	
N_{night}	12	
N_{tag}	20	
Observations	44306	
Marginal R^2 / Conditional R^2	0.001 / 0.002	

Supplementary file 1q. Model output table of model of an individual being awake in a given epoch. The previous night relative total sleep time and previous night relative sleep efficiency variables are standardized. Data that was modelled here was a subset of the full dataset, in which the focal baboon was not awake in the previous epoch, and the current epoch occurred between 21:00 and 05:00 and prior to the 15th day of the study, when several of the baboons' collars ceased collecting data.

		Behavioral scoring		
		Awake		Asleep
		Wakefulness	Resting wakefulness	Sleep
Accelerometer-based sleep classification	Awake	32	89	17
	Asleep	0	41	122

Supplementary file 1r. Confusion matrix reporting the results of the validation study. Table entries represent the number of minute-epochs classified according to the accelerometer-based technique and direct behavioral observation.

Chapter 2: Multi-dimensional social relationships shape the collective dynamics of sleep in wild baboons

Abstract

Sleep is essential for all animals' health and survival, and is largely considered to be an individual experience, most often studied in isolated individuals in laboratory settings. For gregarious animals, however, sleep patterns may critically shape, and be shaped by, the sleep patterns of their group-mates. To shed light on these collective dynamics of sleep, we monitored the nighttime activity and sleep behavior of a group of wild baboons (*Papio anubis*) with infrared computer-vision tracking and tri-axial accelerometry. We found that the sleep patterns of group-mates are inherently intertwined, with cascades of nocturnal waking and collective movement flowing through the group at night. However, wakefulness did not propagate randomly throughout the group, but instead, was guided by the group's affiliative network and, to a much lesser extent, its dominance hierarchy, with individuals exhibiting outsized influence over the nighttime waking of socially affiliated group-mates, as well as subordinate group-mates. Moreover, the effect of the social networks in guiding wakefulness cascades did not arise solely from their potential influence on the spatial distribution of group members within the sleep site. Because of this asymmetric transmission of wakefulness, socially central baboons slept less than their socially peripheral counterparts. Thus, remaining attentive to and engaging with socially relevant group-mates during the sleep period creates costs to sleep investment that are not shared equally across the group. However, this sleep sacrifice may be adaptive, providing socially central individuals more time to maintain the social bonds that contribute to their higher fitness. These results demonstrate that, for group-living animals, sleep is truly a collective behavior, and understanding its adaptive value requires consideration of the complex social dynamics in which it is embedded.

Introduction

Sleep is a biological imperative shared by all animals (Cirelli & Tononi, 2008). Playing a central role in development, central nervous system maintenance, cognitive functioning, and immune defense (reviewed in Zielinski et al., 2016), sleep is a key ingredient to health and survival (Cirelli & Tononi, 2008). However, this period of decreased responsiveness to the outside world often represents

the most vulnerable periods in an animal's daily life, and the trade-off that individuals face when fulfilling this physiological requirement must be carefully negotiated (Lima et al., 2005). Yet, many animals do not navigate this trade-off alone. For social animals, sleep may be fundamentally a collective behavior, whereby an individual's choices about when, where, and how to sleep both shape and are shaped by the choices of their group-mates (Troxel, 2010). However, to shed light on the collective dynamics of sleep, we must investigate sleep in socially relevant contexts, ideally by measuring sleep patterns simultaneously in multiple individuals that share a social environment. This daunting logistical challenge has proven insurmountable to a field of research that has almost exclusively studied the sleep of lone individuals isolated in the laboratory (Aulsebrook et al., 2016; Rattenborg et al., 2017).

Theory predicts that the social environment will have an important influence on the sleep patterns of group-living animals. Sleeping in the safety of a group may enable individuals to sleep longer or more intensely, with perhaps coordinated periods of wakefulness across group members maximizing collective vigilance (Samson et al., 2017). However, evidence suggests that proximity to conspecifics during the sleep period may impede, rather than encourage, high-quality sleep (Loftus et al., 2022; Meadows et al., 2009; Pankhurst & Home, 1994): waves of wakefulness can propagate throughout the group in response to the waking activity of single individuals (Beauchamp, 2009, 2011; Karamihalev et al., 2019; Noser et al., 2003). These costs and benefits of sleeping together, as with many other costs and benefits of group-living (Strauss & Shizuka, 2022), are likely shared unequally across the members of the group. Variation among group members in both their individual traits and social relationships may lead group-mates to experience social influences on their sleep quality quite differently (Karamihalev et al., 2019; Noser et al., 2003). In highly structured societies, in which relationships between group-mates are differentiated and multi-dimensional, an individual's position within the group's multi-layer social network is thus likely to critically influence its ability to obtain a good night's sleep.

To understand how collective dynamics shape the sleep patterns of group-living animals, we investigated the social influences on sleep in wild olive baboons (*Papio anubis*). Baboons live in stable and highly cohesive multi-male, multi-female groups of 15 – 100 individuals (Ray & Sapolsky,

1992), that are comprised of several matrilines (Cheney & Seyfarth, 2008). Complex yet well-studied social dynamics define the lives of baboons (Cheney & Seyfarth, 2008); interactions between group-mates depend heavily on their relatedness, their relative position within the group's linear dominance hierarchy, as well as their affiliative network, which can develop both within and between matrilines (Altmann & Altmann, 1970; Cheney & Seyfarth, 2008). Baboons invest heavily in building and maintaining their highly differentiated and multifaceted social relationships, perhaps unsurprisingly given the importance of these relationships in determining a baboon's fitness (Archie et al., 2014; Campos et al., 2020; Cheney et al., 2016; Silk, 2003; Silk et al., 2009, 2010).

At the end of each day, baboons retreat into tree crowns or onto rock outcroppings, where they spend the night sleeping together (Bidner et al., 2018; Markham et al., 2016). Nocturnal predation by leopards—the primary cause of mortality for adult baboons (Cheney et al., 2004)—places substantial selective pressure not only on the group's choice of sleep refuge, but also on individuals' choices about where to sleep within the refuge. As leopards can infiltrate sleep sites and kill baboons within their refuges (Anderson, 1984, 1998, 2000; Busse, 1980; Isbell et al., 2018), intense competition is expected within the group over preferred sleep locations in the sleep site (Anderson, 1984, 1998; Smeltzer et al., 2022). Dominant individuals may have priority of access to their location of choice, potentially exhibiting outsized influence over the sleep patterns of the individuals that they displace upon relocating within the sleep site during the night. In the safety of the refuge, baboons might also engage in social interactions that allow them to develop and maintain their social bonds, an activity for which they have limited time available during the day (Dunbar, 1992). These potential interactions with affiliated group-mates may further structure the social influence that group-mates have on each other's sleep patterns.

We leveraged high-resolution infrared imagery of a group of wild olive baboons during the night, in conjunction with data from collar-mounted tri-axial accelerometers fit to 26 of the group's members, to investigate the collective dynamics of sleep in a complex society. We monitored the sleep patterns of study group members using an unsupervised classification algorithm that we developed and validated to measure sleep from baboon accelerometry data (Table S2.1). We complemented the sleep data with the nighttime activity and movements of all group members that we

extracted with a computer-vision deep learning algorithm developed to track baboons within the infrared imagery (Table S2.2). Using these data, we assessed sleep as a collective behavior by analyzing interdependencies in the timing of waking and activity across the group during the night. We then explored the mechanism by which social influences on sleep and activity propagate through the group, applying information theoretic and network-based diffusion analyses to understand the role of differentiated, multifaceted social relationships in guiding this propagation. Lastly, we evaluated the outcome of these mechanisms of collective sleep dynamics, testing how an individual's position within the group's social networks influences the time it invests in sleep.

Results

By extracting sleep metrics from 31 calendar days (572 baboon-nights; Table S2.1) of accelerometry data, we found that collared members of the study group slept for an average of 10.7 ± 0.02 (mean ± SE) hours from 18:00 to 06:30, the period when all collars collected data. Individuals woke, on average, 20.0 ± 0.2 times during the night. Infrared computer-vision tracking of the entire group on 21 nights (154.73 total hours of recording; Table S2.2) revealed that baboons occasionally moved during the night, repositioning themselves within their sleep site upon waking (Fig. S2.1).

Sleep and waking patterns during the night indicated that the sleep behavior of group members both influenced and was influenced by that of their group-mates. Collared individuals exhibited synchronization in their sleep states (i.e. sleep vs. waking) during the night beyond that expected by random chance (Fig. S2.2, Fisher's exact test: $p < 0.0001$). Infrared imagery of baboons in their sleep site revealed that periods of synchronized waking during the night were accompanied by collective movement. There were fewer instances than expected during which at least one group member was moving (Fig. 2.1A, Fisher's exact test: $p < 0.0001$), but, when at least one individual was moving, there were significantly more group members moving than expected (Fig. 2.1B, Fisher's exact test: $p < 0.0001$). Additionally, we found that an individual's probability of waking is correlated with the number of individuals that awoke during the previous minute (Fig. 2.1C, Bernoulli generalized linear mixed model (GLMM): standardized estimate [95% credible interval lower bound, 95% credible interval upper bound]: 0.09 [0.02, 0.16]), suggesting that collective waking and movement may involve a sequential diffusion of wakefulness through the group.

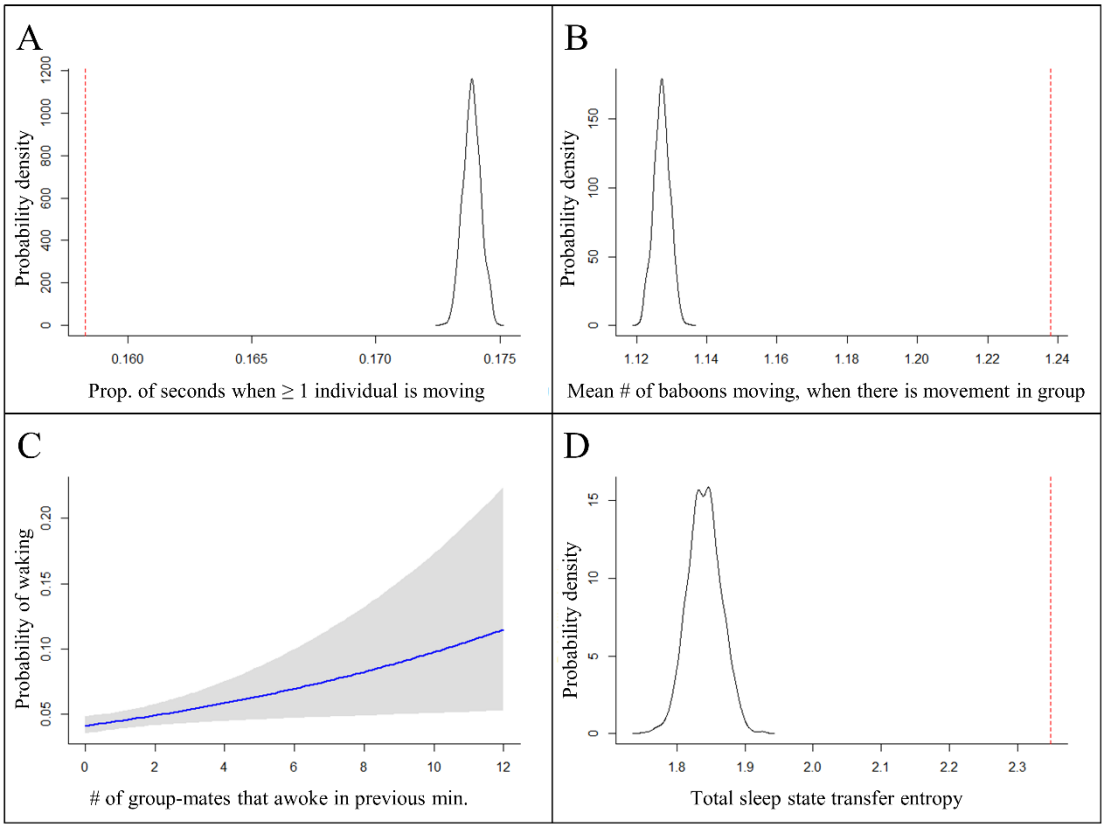

Figure 2.1. The sleep patterns of baboons both influence and are influenced by the sleep patterns of their group-mates. Baboons exhibited temporally coordinated waking and movement during the night. Compared to 1000 time-shifted datasets (A and B, black distributions), there were fewer instances in which any movement was detected in the infrared imagery than expected (A, dotted red line; Fisher's exact test: $p < 0.0001$), but a greater number of individuals were detected as moving, when there was movement within the group (B, dotted red line; Fisher's exact test: $p < 0.0001$). Synchronized periods of movement during the night resulted not from perfectly synchronized awakening, but rather from the sequential awakening of group members, as individuals became increasingly more likely to awaken with the number of group-mates that awoke in the previous minute (C). This transmission of wakefulness caused baboons to have significantly more influence over the sleep states of their group-mates, as measured by transfer entropy (D, dotted red line), than expected based on 1000 time-shifted datasets (D, black distribution, Fisher's exact test: $p < 0.0001$). Subplot (C) depicts the conditional effects from a model of the data.

An analysis of the transfer entropy between the sleep states of group members corroborated a social influence on nighttime sleep patterns. Transfer entropy offers a robust measure of the influence

that one discrete random variable (e.g. an individual's sleep state) has over another discrete random variable (e.g. a group-mate's sleep state). By comparing the sum of the transfer entropies between dyads' sleep states from the empirical data to that calculated from 1000 time-shifted datasets, we found significantly more total transfer entropy between dyads' sleep states in the empirical data than expected (Fig. 2.1D, Fisher's exact test: $p < 0.0001$), indicating that, aggregated across the group, individuals had a significant influence over the sleep state of their group-mates during the sleep period.

Nighttime wakefulness did not spread randomly throughout the group, but rather propagated according to the group's social networks (Fig. 2.2A). We found that group-mates that shared stronger affiliative relationships had greater influence over each other's sleep patterns, such that the dyad that spent the most time together during the day exhibited more than three times as much influence over each other's sleep states, as measured by transfer entropy, than the dyad that spent the least time together during the day (Fig. 2.2B, skew normal LMM: 0.11 [0.03, 0.20]; MRQAP: estimate = 0.197, $p < 0.01$). The social influence on sleep correlated with dominance relationships as well, with individuals having a stronger influence over the sleep patterns of individuals whom they displaced more often during the day (Fig. 2.2C, skew normal LMM: 0.07 [-0.01, 0.16]; MRQAP: estimate = 0.082, $p = 0.07$). However, dominance relationships had a lesser effect than affiliative relationships on influence over sleep state, and we note that the dominance network only approached a significant correlation with the sleep state transfer entropy network in the multiple regression network analysis.

To understand the importance of these social influences on nocturnal awakening, we employed a network-based diffusion analysis, which quantifies the importance of a social network in structuring the diffusion of a behavior (e.g. waking) throughout a group of individuals. We found unequivocal support for both the affiliative network and dominance network in guiding the propagation of wakefulness during the night (summed Akaike weights: affiliative network = 1.0 for all models, relative dominance network = 1.0 for the "tied" model and > 0.95 for "not tied" models; Table S2.3, S2.4). The network-based diffusion analysis revealed that 10.7% [9.1% - 12.0%] of all waking events occur due to the prior waking of a social affiliate, and 4.4% [2.8% - 5.7%] of all waking events occur in response to the prior waking of a dominant group-mate. We also found that

both age and sex influenced the probability of waking in response to the social transmission of wakefulness, as well as the probability of waking independently of other group-mates. Males were more likely to wake, both as a result of social transmission of wakefulness and independent of social transmission, than females (social: males 1.25 [0.97, 1.62] times more likely to wake than females; asocial: 1.08 [1.01, 1.15]). Adults were 1.28 [1.20, 1.37] times more likely than other age groups to wake independently, but were 0.60 [0.43, 0.83] times as likely as other age groups to wake due to social propagation of wakefulness. Juveniles were 0.67 [0.48 – 0.93] times as likely as other age groups to wake due to socially transmitted wakefulness. Thus, subadults were more likely than both adults and juveniles to wake in response to the waking of their group-mates.

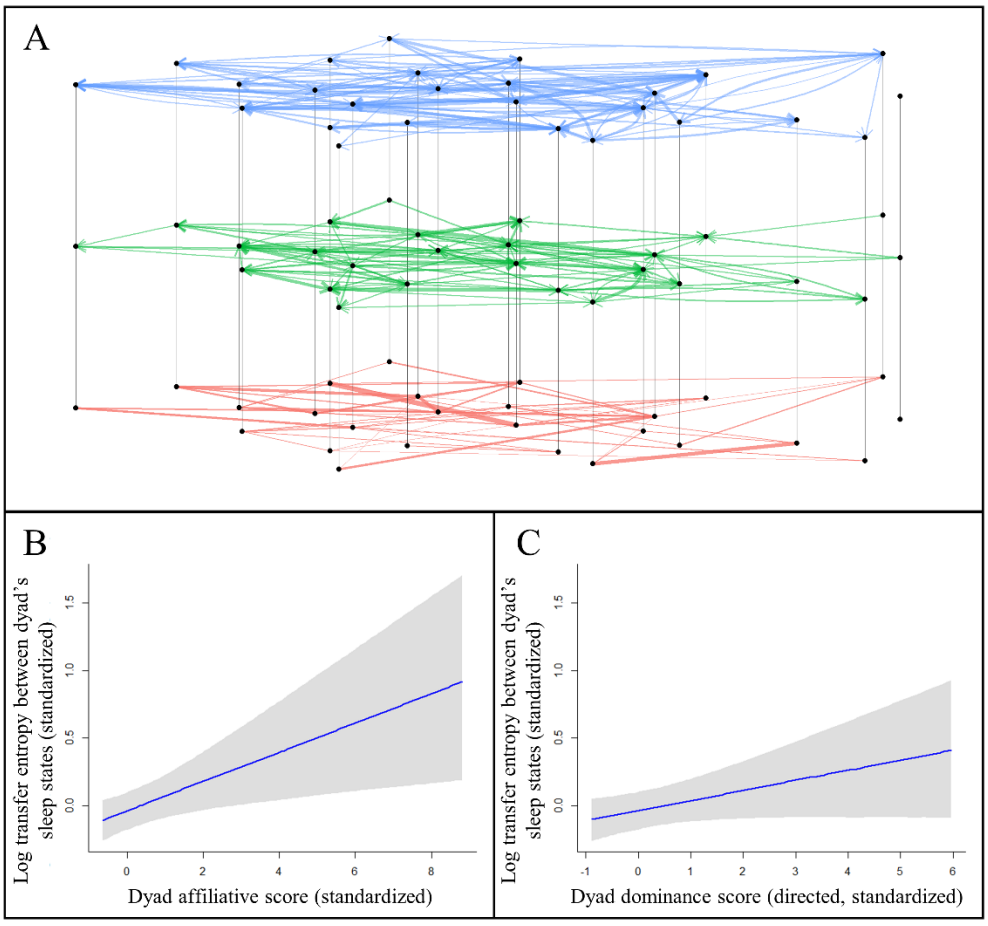

Figure 2.2. Multi-dimensional relationships shape the influence that individuals have over their group-mates sleep patterns. Baboon groups are characterized by highly structured social dynamics in that highly differentiated affiliative (A, red network) and dominance (A, blue network) relationships between group-mates are important in shaping interactions. These social dynamics continue to shape interactions well into the sleep

period (A, green network: sleep state transfer entropy network), as individuals exert greater influence over the sleep patterns of affiliated group-mates (B) and, to a lesser extent, subordinate group-mates (C). In subplot (A), all collared study individuals are represented in each network, with vertical black edges connecting the same individuals across networks. In each network, all edges are weighted, and edges representing values less than the 80^{th} percentile of edge values were removed for plotting, although they were included in the analysis. We note that the affiliative network is undirected while the dominance network and transfer entropy network are directed, with edges pointing from the dominant to subordinate individual in the dominance network and in the direction of the flow of influence in the transfer entropy network. Subplots (B) and (C) illustrate the conditional effects from a model of the data.

We found limited influence of the spatial network on sleep and activity patterns during the night. We predicted that if wakefulness propagated trivially through the spatial network, group members would experience worse sleep on nights when the group's spatial network was denser or less modular, as these spatial constructions would allow more routes through which wakefulness could propagate throughout the network and would prevent wakefulness cascades from remaining localized within a sub-group. However, we found that these properties of the spatial network during the night, which we extracted from the infrared imagery, had no influence on the total time spent sleeping during the night (Fig. 2.3, LMM: spatial network density: -0.33 [-2.17, 1.53], spatial network modularity: -0.40 [-2.22, 1.49]). Moreover, analysis of movement within the infrared imagery suggested that spatial proximity to active individuals might not be sufficient to cause inactive individuals to become active. We found that when individuals became active and relocated within the sleep site during the night, significantly more group-mates subsequently became active in the proximity of locations to which the relocating individuals moved than in the proximity of where they first commenced the relocation (two-sided paired Wilcoxon signed rank test: $V = 1001.5$, $p < 0.02$).

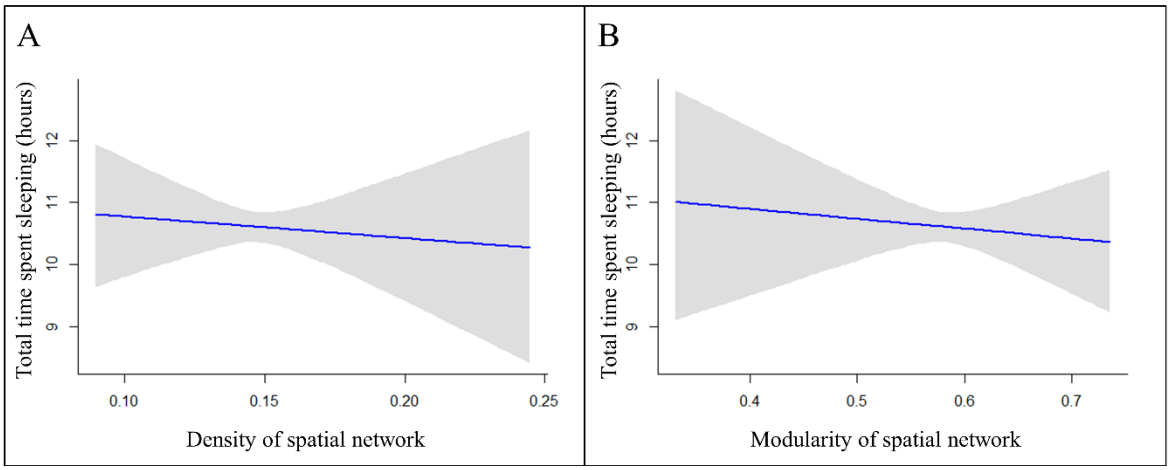

Figure 2.3. Nocturnal wakefulness is insensitive to the arrangement of baboons within their sleep site at night. Neither the density (A) nor the modularity (B) of the spatial network at night influenced the total time that individuals spent sleeping. Because the total sleep time is directly affected by sleep disruptions, this result indicates a limited role of the spatial network in the propagation of wakefulness during the night. Subplots (A) and (B) both illustrate the conditional effects from a model of the data.

The collective dynamics that shaped the sleep behavior of wild baboons had consequences for individuals that were not shared equally across the group. We found that individuals that were more socially connected in the group's affiliative network slept for less total time during the night (Fig. 2.4A, LMM: -0.14 [-0.24, -0.04]). The most socially central individual in the group, according to its eigenvector centrality, slept an average of 16.3 minutes less per night than the most socially peripheral individual in the group. We did not, however, find an effect of an individual's dominance on the total time that it spent sleeping (Fig. 2.4B, LMM: 0.01 [-0.08, 0.11]).

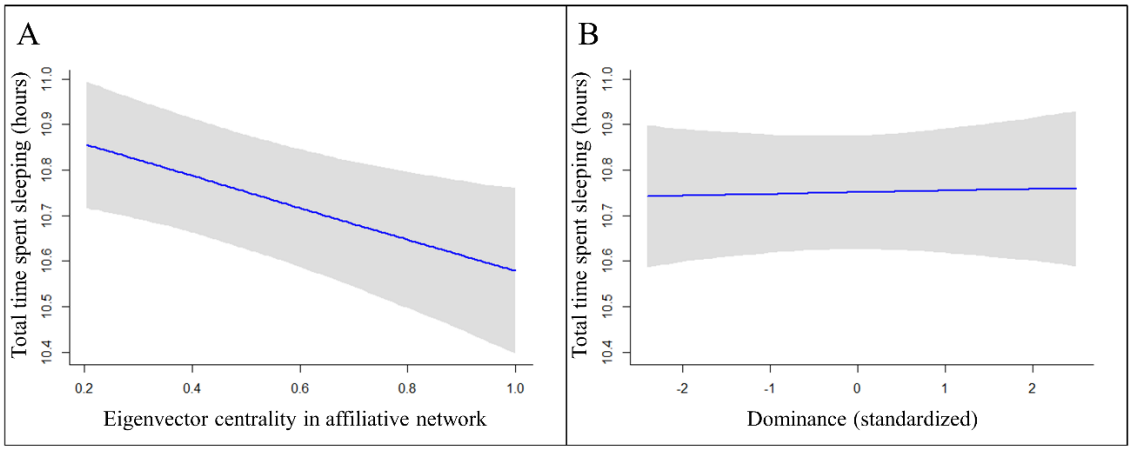

Figure 2.4. Socially central individuals bear the consequences of collective sleep dynamics. With the social transmission of wakefulness propagating primarily through the group's affiliative network, group members that are well connected within the affiliative network, as measured by their eigenvector centrality, obtain less sleep than their group-mates (A). An individual's dominance status, on the other hand, did not influence its ability to obtain sufficient sleep (B). Subplots (A) and (B) both illustrate the conditional effects from a model of the data.

Discussion

We demonstrate that sleep in a wild social primate is characterized by complex collective dynamics, with multifaceted relationships among group-mates forging fundamental interdependencies between their sleep patterns. We show that the social interactions of baboons during the night propagate wakefulness primarily to affiliated group-mates and, to a lesser extent, to subordinate group-mates. Although remaining attentive to a highly structured social environment while sleeping may be important for an animal whose fitness is dependent upon its social relationships (Archie et al., 2014), it leads individuals to sacrifice time invested in sleep—a sacrifice that is disproportionately borne by socially central individuals. Our results shed light on the trade-offs that group-living animals must navigate when reconciling their social priorities with their physiological need for sleep. Thus, this study underscores the importance of investigating sleep in its collective context, where the social relationships that define the interactions between group-mates continue to be crucially important in shaping individuals' behavior during the half of their lives that is spent in darkness.

Decades of research that have implicitly recognized sleep as a strictly individual experience (Gordon et al., 2017; Troxel, 2010). In contrast, our findings demonstrate that, for gregarious animals,

sleep is fundamentally a collective behavior. By fitting the majority of baboons in the study group with collar-mounted accelerometer units and monitoring their sleep patterns during the night with an accelerometer-based sleep classification algorithm, we found that the timing of sleep and wake bouts throughout the night is highly non-random across group-mates. Contrary to the predictions of the sentinel hypothesis, which posits that animals should stagger their periods of nocturnal wakefulness (Samson et al., 2017; Snyder, 1966), we found that baboons' sleep states (i.e. sleep vs. waking) were synchronized. Despite the obvious anti-predator benefits that could be realized by staggering periods of vigilance during the night, sleep synchronization appears to be surprisingly common across taxa (Beauchamp, 2011; Drews et al., 2020; Eban-Rothschild & Bloch, 2012; Karamihalev et al., 2019; but see Samson et al., 2017). However, it has, until now, remained unclear whether synchronized patterns of sleep and waking within a social group arise from simultaneous responses to external stimuli, endogenous rhythms that create stereotyped sleep schedules across individuals, or true social influences on sleep. Here, we demonstrate, with an information-theoretic approach, that synchronization is, indeed, a result of the direct influence that the sleep state of one individual has over the sleep states of its group-mates, and we leverage high-resolution infrared computer-vision tracking to show that synchronized periods of waking during the night are accompanied by collective movements and social interactions within the sleep refuge.

Our findings reveal not only that group members influence the sleep patterns of their group-mates, but that they do so asymmetrically. Specifically, individuals had disproportionate influence over the sleep state of their close affiliates and of subordinate group members. These transfer entropy-identified asymmetries were confirmed with a network-based diffusion approach, which further revealed that wakefulness propagates primarily through the group's affiliative network but also down the dominance hierarchy, with the social transmission of waking through these networks alone accounting for up to 20% of all awakenings during the night (Table S2.3).

Remaining responsive to the behavior of group-mates—particularly that of socially relevant group-mates—during the night may be essential for gregarious animals. Synchronizing activity patterns is important to realizing the full benefits of sociality (King & Cowlishaw, 2009), and coordinating nocturnal waking with social affiliates may reflect an adaptive strategy to maximize the

time available to develop and maintain social bonds—an activity that is important for fitness (Silk, 2003; Silk et al., 2009, 2010), but for which there is limited time available during the day (Dunbar, 1992). We found potential support for this hypothesis (e.g. instances of grooming and copulation during the night; JC Loftus, AC Govaerts personal observations) by using high-resolution infrared imagery to gain unprecedented insights into the nighttime behavior of wild baboons. Monitoring the behavior of dominant group members may also be important for social animals in avoiding aggressive and potentially injurious encounters during the night. This strategy would reflect the strategy adopted during the day, when individuals lend more vigilance to their dominant group-mates to evade confrontational interactions (Treves, 2000).

The social relationships between members of a highly structured society critically shape collective behavior across contexts. In groups on the move, for example, an individual's influence over its group-mates often depends on its affiliative network and relative dominance rank (Jacobs et al., 2011; Papageorgiou & Farine, 2020; Peterson et al., 2002; Sueur et al., 2009). Thus, the distribution of relationships across the group's multi-layer social network has important consequences for collective decisions about where and when to move (Bode et al., 2011a, 2011b; Conradt et al., 2009; Couzin et al., 2005; del Mar Delgado et al., 2018; Strandburg-Peshkin et al., 2018). Baboons, specifically, exhibit outsized influence over the behavior of their social affiliates (Farine et al., 2016; King et al., 2011) and the behavior of subordinate group-mates (Carter et al., 2016; Cheney & Seyfarth, 2008). However, by demonstrating that these multi-dimensional relationships continue to drive interdependencies in group-mate behavior well into the sleep period, we raise the exciting possibility that group-living animals monitor and respond to changes in a complex social environment during the sleep cycle.

An alternative explanation for our findings lies in the possibility that the affiliative network—the network primarily responsible for the social transmission of wakefulness—determines the spatial positioning of individuals within the sleep site. Under this scenario, our results could arise from baboons waking trivially in response to the waking activity of proximate group-mates, regardless of their relationships with those group-mates, per se. Primates have indeed been shown to preferentially sleep in proximity to social affiliates (reviewed in Anderson, 1984), and we have previously

hypothesized that wakefulness propagates via proximity to active individuals (Loftus et al., 2022). Here, by resolving the spatial positioning of group members with infrared videography, we demonstrate that the arrangement of individuals within the sleep site did not influence individuals' sleep duration. This result was contrary to that expected if spatial proximity alone guided the transmission of wakefulness and thus sleep disruptions. Additionally, we found that the movement of an individual within the sleep site during the night precipitated activity in group-mates not at the location where the individual had left, but rather at the location where it relocated. Thus, proximity to an active group-mate, per se, does not necessarily precipitate waking. Instead, wakefulness spreads when active individuals move to, and potentially interact with, socially relevant group-mates. Consistent with this explanation, individuals do indeed engage in interactions during the night upon waking (Packer, 1979; JC Loftus, personal observation). We therefore suggest that the social relationships between group-mates guide the transmission of nocturnal wakefulness within the group, at least somewhat independent of the effect of these relationships on the spatial arrangements of group-mates. However, we note that future extensions of this research that succeed in measuring spatially-explicit social networks will enable a direct test of the independent influences of the spatial arrangement of individuals and the social relationships between them on the collective dynamics of sleep.

Regardless of the precise mechanisms by which wakefulness spreads through the group, the collective dynamics of sleep have consequences for the sleep quality of individual group members, and these consequences are not shared equally across the group. Notably, we show that individuals that are highly connected within the affiliative network sleep less than their less connected group-mates. Thus, social centrality may pose a previously unconsidered burden on individuals aiming to fulfill their daily sleep requirement. This sleep cost of social centrality is a logical consequence of the propagation of nighttime sleep disruptions through the affiliative network and aligns with the recent finding that popularity in human social networks correlates with shorter sleep duration (Li et al., 2019; Mednick et al., 2010). However, the shorter sleep duration of individuals who have strong affiliative relationships, taken together with the health detriments of insufficient sleep (Durmer & Dinges, 2005;

Knutson et al., 2007; Mullington et al., 2009), appears to be in conflict with the higher fitness that socially connected individuals experience (Cheney et al., 2016; Silk et al., 2009).

We suggest three potential explanations for the logical inconsistency that socially central baboons experience higher fitness despite sleeping less. First, it is possible that although socially central group members sleep for a shorter duration, other aspects of their sleep improve. Socially connected humans, for example, experience more efficient, less fragmented sleep than their socially isolated peers (Cacioppo et al., 2002; Kurina et al., 2011). Human couples also report better subjective sleep quality—which proves important in achieving the health benefits of sleep (Buysse, 2014)—when sleeping together compared to when sleeping apart, despite objective indicators suggesting the reverse pattern (Pankhurst & Home, 1994). Although it may not be possible to assess an animal's subjective experience of sleep, further investigation should evaluate whether socially connected individuals compensate for shorter duration sleep with improvement in other characteristics of their sleep (e.g. sleep fragmentation, sleep efficiency). Second, it is possible that socially central individuals do indeed experience worse overall sleep quality than peripheral individuals, and that incidental costs of lost sleep for socially central individuals are compensated by other fitness benefits of strong affiliative relationships, including enhanced offspring survival (Cameron et al., 2009; Silk, 2003), increased mating opportunities (Schülke et al., 2010), and increased tolerance at feeding patches (King et al., 2011). Lastly, we propose that the shorter sleep duration of socially connected individuals may not represent an incidental cost at all, but rather reflect a strategy of adaptive sleep loss (Lesku et al., 2012), with individuals willingly giving up sleep to invest in maintaining their social network. Thus, the costs of lost sleep may be recouped directly within the sleep period by trading high-quality sleep for the fulfillment of social needs (Troxel, 2010). This final possibility highlights the trade-off that group-living animals face when balancing the benefits of strong social bonds with their physiological sleep imperative, and supports recent findings from ecologically-relevant settings that have revealed that animals often sacrifice sleep to perform other fitness-critical behaviors in the wild (Basner et al., 2007; Lesku et al., 2012; Loftus et al., 2022; Rattenborg et al., 2016).

Interestingly, we did not find an influence of social dominance on sleep duration, despite the flow of wakefulness down the dominance hierarchy. This result likely reflects the relatively minor role that the dominance network played, in comparison to the affiliative network, in guiding the propagation of awakening within the group. The relative importance of the affiliative and dominance networks in shaping sleep dynamics reflects findings from contexts outside of the sleep period, which suggest that affiliative bonds may be more important than dominance relations for an animal seeking to meet its daily needs (Cheney et al., 2004; Marshall et al., 2015; McFarland et al., 2017; Sick et al., 2014; Silk et al., 2010).

Continuing to unravel the collective dynamics of sleep may prove critical in understanding broader connections between social behavior, sleep, and health in our own species. A burgeoning research interest at the intersection of sleep and social behavior in humans has revealed intriguing bi-directional feedbacks: poor sleep can impair social functioning, while social stressors and deficiencies can impair sleep quality (poor sleep leads to impairments in the following social functions: greater interpersonal conflict (Gordon & Chen, 2014), social isolation (Ben Simon & Walker, 2018), lower empathetic accuracy (Gordon & Chen, 2014; van der Helm et al., 2010), reduced engagement in social activity (Holding et al., 2020), and increased social stress (Prather et al., 2013; Radwan et al., 2021); the following social stressors and deficiencies lead to poor sleep: interpersonal conflict (Hicks & Diamond, 2011), social isolation (Cacioppo et al., 2002; Kurina et al., 2011), and low social capital (Robbins et al., 2019); reviewed in Gordon et al., 2017, 2021)). Understanding the link between sleep and social behavior is a public health priority given that sleep disorders and impairments in social functioning often present comorbidly (Spoormaker & Montgomery, 2008; Steiger & Kimura, 2010), and that both of these pathologies have been implicated as causes of a variety of downstream health concerns (Barnes & Drake, 2015; Seeman, 1996). Yet, despite clear interdependence between our sleep and our social world, exceptionally few studies have considered the role of social dynamics that occur *while* we sleep (but see Troxel, 2010; Troxel et al., 2007). Although modern humans may not sleep in the large aggregations typical of many other social animals, our earliest ancestors likely did sleep in conditions quite similar to those of modern baboons, as early hominins moved into their new niche in the expanding savannahs (Brain, 1983; Isbell et al., 2018). Investigating the collective

dynamics of sleep in the social and ecological environment in which it evolved may generate key insights into *why* our social behavior and our sleep are so intertwined. This functional perspective could prove critical in generating solutions to disrupt the self-reinforcing cycle between poor sleep and social dysfunction that impacts the one in three Americans that are sleep deprived (Sheehan et al., 2019).

Materials and Methods

Data collection

We monitored sleep patterns and nighttime behavior in a group of wild olive baboons at Mpala Research Centre, a 200 km^2 conservancy comprised of savannah-woodland habitat on the Laikipia Plateau in central Kenya. From July 15 to July 18, 2019, we captured members of the study group in individual traps that were placed near the study group's primary sleep site and baited with maize. Trap baiting began two weeks before capture to habituate baboons to the traps. Individuals that were clearly too small to be fit with a telemetry device were released upon capture. We anesthetized the remaining 28 baboons with 10 mg/kg of ketamine hydrochloride (Bremer Pharma GmbH, Warburg, Germany) and 0.03 mg/kg of medetomidine (Domitor, Zoetis Ltd., Parssipany-Troy Hills, NJ, USA), visually estimating body mass to determine the appropriate dosage. Upon immobilization, we weighed each individual and estimated its age-class according to its body size and secondary sexual characteristics (Altmann et al., 1981). Of the 28 individuals anesthetized, all but one were large enough to be fit with a telemetry collar, such that the collar was less than 3% of its body weight. See Kamau et al. (2021) for further details on the health monitoring of baboons during and after anesthesia.

We fit GPS collars with an integrated tri-axial accelerometer (e-Obs Digital Telemetry, Gruenwald, Germany) to 27 baboons in the study group. Adults and large subadults were fit with collars containing a D-cell battery, while small subadults and juveniles were fit with collars containing a C-cell battery. We painted the battery casing of each collar with a unique color combination to facilitate individual identification. Collars began collecting data on July 19, 2019, and the 27 collars deployed were split among two different sampling regimes. We programmed 11 collars (collar ID's beginning with "2" in Table S2.1) to collect GPS locations at 1 Hz and continuous tri-

axial accelerations at 12 Hz/axis from 06:30 to 18:00, and 0.71-second bursts of accelerations at 56.2 Hz/axis at the beginning of every minute from 18:00 to 06:30. These 11 collars were not programmed to collect GPS data from 18:00 to 06:30. One of these 11 collars failed to collect any data. The remaining sixteen collars (collar ID's beginning with "6" in Table S2.1) collected GPS locations at 1 Hz from 06:30 to 18:00 without accelerometry and, from 18:00 to 06:30, they collected 2-second bursts of accelerations at 20 Hz/axis and a GPS location every five minutes when the accelerometry indicated that the baboon was moving or every ten minutes when the accelerometry indicated that the baboon was stationary. C-cell collars with this sampling schedule were reprogrammed to collect high-resolution GPS data from 06:30 to 10:00 and lower-resolution GPS and accelerometry burst data from 10:00 to 06:30 beginning on August 6. On August 15, the D-cell collars with this sampling schedule were reprogrammed to collect a 2-second burst of accelerations every five seconds during the night, as opposed to every minute. We programmed collars to continue collecting data until they were released from the baboons via an automatic break-away unit (SureDrop, Advanced Telemetry Systems, Isanti, MI, USA) on August 18, 2019, although the actual duration of data collection varied by collar (see Table S2.1). In total, we collected 649 baboon-nights of accelerometry data, with night defined as the period from noon to noon.

We monitored the behavior of group members during the night, starting when they approached their sleep site, using a high-resolution infrared camera (FLIR T1020, FLIR Systems Inc., Wilsonville, OR, USA) that was mounted in a fixed location across from the study group's primary sleep site. We recorded 1024x768 resolution infrared images at 5 Hz on each night of recording for as long as the camera battery allowed (average recording duration [range of recording durations]: 7.4 hours [1.7 – 13.9 hours]; Table S2.2). We collected infrared recordings every night that the study group inhabited their primary sleep site from July 31 to August 21, 2019, for a total of 21 nights (154.73 hours) of infrared imaging data (Table S2.2).

We monitored the daytime activity of members of the study group every morning, shortly after they departed from their sleep site, with video recorded from four GoPro Hero 7 cameras (GoPro Inc., San Mateo, CA, USA) mounted 5 meters high on stationary tripods. The aerial-perspective enabled us to simultaneously record the behavior of as many group members as possible. The GoPro

cameras recorded with 1920x1080 resolution at a frame rate of 24 frames per second. We recorded videos every morning from August 2 to August 15, 2019 for approximately one to two hours.

Sleep measurement from accelerometry

We used the accelerometry data to classify sleep behavior using an algorithm that we adapted from a method that we had previously developed and validated for use in measuring sleep in baboons (Loftus et al., 2022). The algorithm, which was itself adapted from a method developed by van Hees and colleagues (2015, 2018) to classify sleep and the sleep period in humans, could not be applied to the current dataset in its original implementation because the accelerometry sampling schedule deviated from the requirements of the original implementation.

To algorithmically classify sleep from the accelerometry data, we first down-sampled and interpolated the accelerometry data to match the most limited sampling schedule and rate across the accelerometer units, uniformizing the effective sampling across devices. After this processing, each of the 26 individuals had 0.67-second bursts of 12 Hz/axis accelerometry data every minute on the minute from 18:00 to 06:30. For each accelerometry burst, we calculated the vectorial dynamic body acceleration (VeDBA) using a 0.42-second time-window and then calculated the mean VeDBA over the burst. We log-transformed these mean values to derive the mean log VeDBA (henceforth, log VeDBA) for each burst. We then classified periods of at least three minutes, during which an individual's log VeDBA never exceeded the 90th percentile of its log VeDBA across the study period (limited to 18:00 to 06:30, by the data processing step above) as sleep. All minute epochs within the 18:00 to 06:30 period that did not meet these criteria to be considered sleep were classified as waking behavior. This data processing resulted in a total of 646 baboon-nights of sleep data.

From the sleep data, we extracted both the minute-by-minute pattern of sleep and waking behavior of each collared individual, as well as the total time that each collared individual slept during each night, calculated as the total number of epochs classified as sleep within the 18:00 to 06:30 data collection period. Because the total time spent sleeping was potentially underestimated when accelerometer units occasionally failed to record an accelerometry burst, we removed data for total sleep time on nights during which an individual was missing a total of at least 45 (> 6%)

accelerometry bursts during the 18:00 to 06:30 period. This filtering removed 74 baboon-nights of data, for a total of 572 baboon-nights of data on total sleep time for analysis.

Validation of sleep classification algorithm

To validate that the sleep classification algorithm accurately measured sleep behavior, we compared its classification of sleep to observer-identified sleep and waking behavior of baboons in the study group. Using the infrared recordings, we performed behavioral observations of study individuals within their sleep site following the initial data collection. We identified study individuals for observation within the infrared imagery using both real-time narration of the recordings, as well as post-recording matching of the positions and movements of individuals within the infrared imagery to the GPS and accelerometry data of collared individuals. For the duration during which a collared individual was identifiable, an observer categorized the individual's sleep state as representing "wakefulness", "resting wakefulness", or "sleep," following the definitions provided in Loftus et al. (2022). This procedure resulted in a total of 15.3 hours of observation across 19 study individuals. The behavioral observations were recorded using the commercial software Loopy (Loopbio GmbH, Austria) and the open-source software BORIS 7.9.4 (Friard & Gamba, 2016).

Using the direct observations in the infrared imagery, we extracted a validation set of a total of 650 epochs that were both classified as wakefulness or sleep by the sleep classification algorithm and declared as wakefulness, resting wakefulness, or sleep by the human observer. Categorizing both wakefulness and resting wakefulness as waking behavior and considering the observer-identified sleep and waking behavior as the true sleep state, we found that the sleep classification algorithm had an accuracy of 73.5% (Table S2.5).

Measuring social relationships

After initial data collection, we performed behavioral observations in the videos that we recorded in the morning, following the group's departure from their sleep site. We identified individuals within the videos with collar-derived GPS track overlays on the original videos, in conjunction with concurrent photographs taken from a terrestrial perspective (as opposed to the aerial perspective of the videos) and real-time narration of the videos that clarified the unique color combination on the collars of individuals in the field-of-view of the video. We used a focal follow

sampling procedure (Altmann, 1974) to record the behavior of collared individuals that we identified in the videos, which resulted in a total of 15.8 hours of focal observations across 23 collared individuals. From these focal observations, we extracted instances in which the focal individual engaged in co-sitting with a group-mate or displaced (or was displaced by) a group-mate. We defined co-sitting as stationary behavior occurring within an arm's length of a group-mate and displacement as an individual moving towards a group-mate and taking the position of this group-mate, causing the group-mate to move away from its original position. We noted the identity of the non-focal individual, when possible, during these dyadic behaviors. In total, we identified 185 distinct periods of co-sitting and 94 displacements in which both individuals involved in the encounter were collared.

We then paired these observations with features from the GPS and accelerometry data to train a decision-tree machine-learning model with extreme gradient boosting, using the classification learner toolbox in MATLAB 2020 software. We included the following features in the model: the mean speed of each individual, proportion of time each individual is non-stationary (based on stationary vs. nonstationary model prediction), each individual speed change (by fitting linear slope), speed difference among individuals (at the beginning, end, and mean), dyad distance characteristics (at beginning, end, mean, minimum, fitted linear slope), angular difference in movement direction between the two individuals and dynamic time warping score based on the trajectories. We split the data into training dataset and testing dataset with 5-fold cross validation. The model exhibited 88% accuracy in identifying co-sitting and 81% accuracy in identifying displacements. We then applied the model to predict instances of co-sitting and displacements in the full dataset. Because co-sitting is an affiliative behavior (Farine et al., 2016; King et al., 2011), we used the predicted instances of co-sitting from the full dataset to defined a dyad's affiliative relationship (also referred to in the text as affiliative score) as the total amount of time they spent co-sitting over the study period divided by the amount of time during which we collected data from both dyad members. The group's affiliative network represents the concatenation of all dyad's affiliative relationships. As displacements (i.e. approach-avoid interactions) often reflect broader dominance relationships (Sapolsky, 1983; Seyfarth, 1976), we defined a dyad's dominance relationship as the total amount of time that one individual spent displacing the other dyad member, divided by the amount of time for which we collected data

from both individuals. We note that we calculated the dominance relationship values for each dyad directionally. We used these dominance relationships to create two dominance networks for the group: the absolute dominance network included all dominance relationship values for all dyads, whereas the relative dominance network included only positive values of the net dominance relationships (i.e. ID A's dominance value over ID B minus ID B's dominance value over ID A).

Extracting nighttime spatial positioning and individual movement from infrared imagery

We used the FLIR File Science Software Development Kit (https://flir.custhelp.com/app/account/fl_download_software) for Python to extract infrared imaging data from its proprietary file format and to divide each night's infrared recording into hour-long segments for ease of processing. From the infrared imagery, we also extracted 976 individual frames that were distributed across the data collection period, and, in each frame, we localized all present baboons and annotated them with bounding boxes using the commercial software Loopy (Loopbio GmbH, Austria; Fig. S2.3A). This procedure produced a total of 28556 annotations, 22000 (77.0%) of which were used to train a convolution neural network (CNN) to detect baboons within the infrared imagery. Specifically, we used Facebook's Detectron2 application programming interface (API; Wu et al., 2019) within the PyTorch framework (Paszke et al., 2019) to fine-tune a Faster-RCNN (Ren et al., 2016) with a Resnet 50 Feature Pyramid Network backbone (Lin et al., 2017) that was pre-trained on the Common Object in Context (COCO) dataset (Lin et al., 2014). We chose a learning rate of 0.005 and allowed a maximum of 4000 iterations. We validated the model on the remaining 6556 (23.0%) annotations, revealing a model recall of 0.71 and precision of 0.18 with a score (i.e. model confidence) threshold of 0.60 and intersection-over-union (IOU) threshold of 0.50 (Fig. S2.4), and a model recall of 0.59 and precision of 0.19 with a score threshold of 0.80 and IOU threshold of 0.50 (Fig. S2.5). We applied the trained CNN to detect all baboons in each frame of the full dataset of infrared recordings from the study period (Fig. S2.3B), taking the mean of the four corners of each bounding box prediction to be the location of a baboon in the frame. We predicted the location of baboons in each frame with the CNN using two different score thresholds: 0.60, which we used to measure the spatial networks of the group during the night, and 0.80, which we used for tracking the baboons while within their sleep site. Although setting the threshold to 0.80 compromised recall

without a notable advantage in precision, user-experience suggested that this threshold setting facilitated the manual corrections of tracks (see below).

To extract continuous tracks for every individual in the infrared imagery from the CNN-detected positions on each individual frame, we connected consecutive positions that corresponded to the same baboon across frames into trajectories (Fig. S2.3C). We constructed individual trajectories with a modification of the Hungarian method (Kuhn, 1955), in which we extended each track (starting as a single location for each detected baboon in the first frame) frame-by-frame by assigning positions in the current frame to existing tracks such that we minimized the total distance between the most recent position of each track and its newly assigned position. However, we applied the Hungarian algorithm under the constraint that a track could not be assigned a position that was farther than 100 pixels or 0.45 times the distance to the closest track away from the focal track's most recent location. When two tracks were in close proximity, we allowed a minimum new position search radius of 10 pixels to override the aforementioned constraint. We allowed tracks to persist as candidates for extension for 30 frames after their most recent new position assignment, after which they were considered to be completed. If a new position was assigned to a track that was not assigned a position in the previous frame, linear interpolation provided the locations of the track between its most recent position and the newly assigned position. When a new position was not assigned to an existing track, this new position became the start of a new track; but if the algorithm did not assign subsequent positions to this newly instantiated track with sufficient frequency, the new track was automatically deleted. In a customized graphical user interface, we then manually corrected tracks for errors to produce human-verified, error-free tracks of each baboon's movement in the infrared recordings. Because we processed infrared recordings for position detection and tracking in one-hour segments, we merged tracks that terminated at the end of a recording segment with the closest track within 25 pixels that commenced at the beginning of the next consecutive recording segment within each night. Thus, we were able to produce continuous tracks for each baboon that persisted for as long as the individual was in view during the duration of infrared recording. Due to the labor-intensive nature of the manual track corrections, we only corrected a subset of all tracks, which produced a total of 23.5 hours of corrected tracking data across seven nights. In analyses that were not sensitive to minor

errors in the tracks (noted in *Statistical analysis*), we used the uncorrected tracks instead of the manually corrected tracks to augment sample size.

Prior to analysis, we applied a spatial correction to the position and track coordinates extracted from the infrared imagery in order to ameliorate the distortion caused by the perspective with which the video was recorded. During data collection, we recorded a cylindrical object of known dimensions as we moved it across the field of view of the camera. When depicted in the two-dimensional recording, the cylindrical object appeared as a rectangle whose width was insensitive to the exact orientation of the cylinder. Using ImageJ software (Schneider et al., 2012), we extracted the image coordinates of the corners of the apparently rectangular object at several locations within the field of view (Fig. S2.6A). From these coordinates, we calculated the length, in pixels, of the line segments forming the left and right sides of the rectangles, as well as the image coordinates of the midpoint of each such line segment. We then modelled the length of the line segments as a function of the x-coordinate of the midpoint of the line segments. Because the relationship between the x-coordinate of the midpoint of a line segment and its length was approximately linear, we used a first-order linear regression model. This regression produced the following equation:

$$l = 0.0169x + 8.762, \tag{1}$$

where l is the length, in pixels, of the line segment representing a side of the measurement object and x is the x-coordinate within the image of the midpoint of the line segment. This equation can be used to find the metric dimensions of a pixel as a function of its x-coordinate because

$$lp = s \tag{2}$$

where l is still the length, in pixels, of the line segment representing a side of the measurement object, p is the metric length (and width) of a pixel, and s is the metric length of the side of the measurement object and is, therefore, constant. Solving for p as a function of x, we find:

$$p = \frac{s}{l} = \frac{s}{0.0169x + 8.762} \tag{3}$$

To find a corrected x-coordinate that amends the distortion caused by the variable metric dimensions of a pixel, we simply integrate equation (3) for the size of a pixel as a function its x-coordinate from 0 to our initial x-coordinate. Thus,

$$x_c = \int_0^{x_o} \frac{s}{0.0169x+8.762} dx \tag{4}$$

Because

$$\int \frac{1}{ax+b} dx = \frac{log|ax+b|}{a} + constant, \tag{5}$$

we find,

$$x_c = s \frac{log|0.0169x+8.762|}{0.0169} \Big|_0^{x_o} \tag{6}$$

where x_c is the spatially corrected x-coordinate, x_o is the initial x-coordinate, and s is still the metric length of the side of the measurement object, which we measured to be 0.4064 m.

To find the corrected y-coordinate, we first centered each y-coordinate by subtracting the mean of the y-coordinates. We then multiplied each centered y-coordinate by the metric length of a pixel, as determined by evaluating equation (3) at its associated x-coordinate. Thus,

$$y_c = y_e \frac{s}{0.0169x_o+8.762} \tag{7}$$

where y_c is the spatially corrected y-coordinate, y_e is the centered y-coordinate, and x_o is the initial x-coordinated associated with this y-coordinate.

Because the spatial correction is applied based on the x-coordinate of each location, it is important that locations with the same x-coordinate are equidistant from the infrared camera. Due to the perspective of the camera, this prerequisite was not necessarily met. Thus, before performing the spatial correction procedure described here, we rotated the tracking coordinates, as well as the coordinates of the corners of the measurement object by a rotation matrix that ensured that the x-coordinates were proportional to the distance from the camera (Fig. S2.6B). Specifically, in ImageJ, we marked several locations along the cliff ledge that is parallel to the horizontal plane, but does not appear to be in the infrared imaging. We modelled a linear regression of these locations, which produced the equation:

$$y = -0.486x - 958.40 \tag{9}$$

Using the slope from this regression line, we found the angle needed for rotation, as

$$a = |tan^{-1}(-0.486)|, \tag{10}$$

where a is the angle of rotation. We then applied the following rotation matrix to the coordinates of the tracks, as well as the coordinates of the measurement object before proceeding with the spatial correction:

$$\begin{bmatrix} x_o \\ y_o \end{bmatrix} = \begin{bmatrix} cos\, a & -sin\, a \\ sin\, a & cos\, a \end{bmatrix} \begin{bmatrix} x_r \\ y_r \end{bmatrix} \quad (11)$$

where x_o and y_o are the initial x- and y-coordinates used as input for the spatial correction, and x_r and y_r are the raw x- and y-coordinates, respectively.

After applying the spatial correction to the tracks extracted from the infrared recordings (Fig. S2.6C), we smoothed the tracks to reduce error and to decrease the location sampling frequency to a more biologically relevant timescale. We smoothed the tracks by reducing them to their mean x and y location for each second, effectively decreasing the location sampling frequency from 5 Hz (the frame rate of the infrared camera) to 1 Hz. We then calculated the speed of each track.

While performing the behavioral observations in the infrared imagery for the validation of the sleep classification algorithm (see *Validation of sleep classification algorithm*), we also recorded the position state of each focal individual as "lying down", "crouching", "sitting", "standing (quadrupedally)", "standing (bipedally)", "walking", "running", "climbing", or "other". We categorized "lying down", "crouching", "sitting", "standing (quadrupedally)", and "standing (bipedally)" as stationary behavior, and "walking", "running", and "climbing" as non-stationary behavior. We paired these observations with the speed of the associated track to train a decision-tree machine learning model with extreme gradient boosting that predicted whether an individual in the infrared imagery was exhibiting stationary or non-stationary behavior, using track speed as the sole feature. We extracted 12,971 second epochs during which we were able to both calculate the speed of an individual's track and determine whether it was stationary or non-stationary by direct observation. We performed a class balanced split of the labelled dataset using the "caret" package (Kuhn, 2008) in R software version 4.1.3 (R Core Team, 2022) to produce a training set of 10,377 (80%) epochs and a test set of 2,594 (20%) epochs. Prior to training the model, we removed epochs from the training set (but not the test set) in which the individuals were not actually on the main rock outcropping within their sleep site, as these locations were not only unlikely to have been corrected by the spatial

correction we applied, but they were likely actually further distorted by the correction. This exclusion reduced the number of training epochs to 10,258. We did not exclude these locations from the test set, so that we could generate a confusion matrix that would be representative of application of the model predictions to the full dataset. After training, the model exhibited an accuracy of 99.7% in its classification of stationary and non-stationary behavior in the test set (Table S2.6). We used the "xgboost" package (Chen et al., 2015) via the "caret" package (Kuhn, 2008) in R software to train and evaluate the model. We processed the full dataset (both for manually corrected as well as uncorrected tracks) with the model to predict whether tracks were stationary or non-stationary during each second.

Statistical analysis

We tested whether collective dynamics influenced baboon behavior during their sleep period by investigating whether baboons exhibited coordinated patterns of nighttime waking and movement within their sleep site. We limited these analysis to the period from 21:00 to 05:00, as these times fall well within the sleep period of wild baboons (Loftus et al., 2022). We first tested for synchronization in collared individuals' sleep-wake patterns, extracted with accelerometry-based sleep classification (see *Sleep measurement from accelerometry*), by measuring the proportion of group members that exhibited the majority behavior (either sleep or waking) during each minute epoch. We took the mean over all epochs to calculate the mean proportion of the group that is synchronized in their sleep state across the study period. We compared this empirical value to a null distribution produced by calculating the mean proportion of the group that is synchronized in their sleep state in each of 1000 time-shifted datasets. We evaluated significance with a one-sided Fisher's exact test, where the p-value represents the proportion of the values in the null distribution that are as great or greater than the empirical value. To investigate whether synchronized waking events reflected collective movement within the sleep site, we tested the prediction that movements coordinated across group-mates during the night would result in concentrated collective movement events (i.e. fewer instances across the night than expected by chance when at least one individual was moving) during which more individuals would be moving than expected by chance. We used the stationary vs. non-stationary classification of the tracks in the infrared imagery to calculate the proportion of seconds during the study period (again from 21:00 to 05:00) in which at least one individual was moving. We

also determined the mean number of individuals that were moving when there was any movement within the group. We compared these empirical values to null distributions generated by calculating 1000 replicates of the same values, each computed after applying a random time shift to each individual's track. By shifting the data in time, rather than permuting the time-series, we preserved the autocorrelation structure of each individual's empirical data in the null distribution. We tested for significance with a one-sided Fisher's exact test. Spurious significant results indicating collective movement during the night may result from individuals being synchronous not necessarily in their periods of non-stationary behavior, but rather simply in when their tracks are visible in the infrared imagery. However, using the same time shifting procedure described above, we found that tracks were not more synchronized, but rather less synchronized in their presence – indicated by a significantly lower standard deviation in the number of tracks present at any given time across the study period – in the empirical data than in the time-shifted data ($p < 0.0001$; Fig. S2.7), eliminating the concern of a spurious significant result. Because this analysis of the infrared tracking data was not sensitive to small errors in the tracking (e.g. track identity switching, track fragmentation), we used the tracks that had not been manually corrected to augment sample size.

To understand whether periods of collective waking and movement during the night actually reflected social influences on sleep or, rather, synchronized responses to exogenous stimuli, we investigated the temporal dynamics of changes in sleep state across the group. We first tested whether the waking of group-mates increased the likelihood of a focal individual waking in the following minute. Presuming that a baboon's reaction time is less than a minute, we predicted that there would be no correlation between the number of individuals that awoke in the previous minute and the probability of a focal individual waking if the causes of collective waking were purely extrinsic to the group. We used a Bayesian generalized linear mixed model (GLMM) of family Bernoulli to model the probability of transitioning from sleep to waking in a given minute as a function of the number of individuals that awoke during the previous minute. We included a fixed effect spline variable for minutes since 18:00 to control for intrinsic periodicity in the baboons' sleep cycles that may increase their likelihood of awaking at similar times during the night, as well as random intercepts for individual and night identity. Before model fitting, we downsampled the data to every 15^{th} observation

to eliminate the autocorrelation in the response variable (Fig. S2.8) and to avoid the excessive run time associated with directly modelling the autocorrelation of the response variable (a model that explicitly incorporated autocorrelation had not reached 10% of its run time after seven days). We limited this analysis to the period from 21:00 to 05:00 and to nights prior to August 10, 2019, as the analysis is sensitive to the number of individuals with functioning collars, and, on August 10, 2019, the number of functioning collars drops and remains below 75% of the original number of functioning collars.

We analyzed the transfer entropy between the sleep states of study group members for a more detailed understanding of how an individual's sleep and waking behavior both influences and is influenced by the behavior of each of its group-mates during the sleep period. Transfer entropy is a conditional mutual information measure that can be expressed as:

$$TE_{X\to Y} = I(Y_t;\, X_{t-1:t-L} | \, Y_{t-1:t-L}), \tag{12}$$

where $I(X;\, Y|\, Z)$ is the mutual information between random variables *X* and *Y*, conditioned on the random variable *Z*. Thus, the transfer entropy from individual X's sleep state (asleep vs. awake) to individual Y's sleep state represents the information shared between individual Y's current sleep state and individual X's past *L* sleep states that is not already contained in individual Y's past *L* sleep states. A perhaps more intuitive formulation is provided by the further decomposition of the conditional mutual information:

$$TE_{X\to Y} = H(Y_t | \, Y_{t-1:t-L}) - H(Y_t | \, Y_{t-1:t-L}, X_{t-1:t-L}), \tag{13}$$

where $H(X)$ represents the Shannon entropy of the random variable *X*. Because the Shannon entropy of a random variable, given by:

$$H(X) = -\sum_{x \in X} P(x) \log \mathrm{P}(x), \tag{14}$$

measures the uncertainty of the random variable *X*, equation (13) can be read as: the transfer entropy from *X* to *Y* is equal to the reduction in uncertainty about the current (sleep) state of *Y* that we achieve by knowing the past *L* states of *X*, given that we already know the past *L* states of *Y*. For our purposes, the transfer entropy can be thought of as the influence that one individual's sleep behavior has on the

sleep behavior of a particular group-mate. We note that transfer entropy is a directional measure, such that:

$$TE_{X \to Y} \neq TE_{Y \to X} \quad (15)$$

We first assessed whether individuals indeed influenced their group-mates' sleep behavior by comparing the transfer entropy between group members' sleep states to that expected by random chance. We measured the transfer entropy between the sleep states of each dyad over the study period, again limited to the 21:00 to 05:00 period, and summed these entropies across the dyads within the group to calculate an empirical value of the total transfer entropy within the network. We then calculated this same value, but after randomly time-shifting the data of one of the dyad members, repeating this procedure for a total of 1000 times to generate a null distribution. We compared the empirical value of the total transfer entropy within the network to its null distribution with a Fisher's exact test. For all transfer entropy calculations, we used a history length (L in equations (12) and (13)) of 3 because the autocorrelation in individual's sleep state during the 21:00 to 05:00 period appeared to dissipate at lag 3 (Fig. S2.9), suggesting that the Markov order of the sleep state time-series does not exceed 3.

We then analyzed how the relationships between individuals affect the influence they have over each other's sleep behavior. Specifically, we tested how dominance and affiliative relationships influence transfer entropy in sleep state. We modelled the log of the empirical transfer entropy between dyads' sleep behavior over the study period using a Bayesian GLMM of the skewed normal family. We included the dyad's dominance score (directed) from the absolute dominance network and affiliative score (undirected) as fixed effects in the model, and the identity of each dyad member and the identity of the dyad itself as random intercepts in the model. We standardized the response variable and fixed effects variables, by subtracting the mean and then dividing by the standard deviation, before model fitting. Despite the implicit violation of independence in network data, we opted to model the data with a GLMM so that we could extract, and draw conclusions from, the effect sizes of the fixed effect variables. However, we confirmed our results with appropriate network statistics. We implemented the multiple regression quadratic assignment procedure (MRQAP) with double-semi-partitioning (DSP) and 1000 randomizations in the package "asnipe" (Farine, 2013) in R

to test for an effect of the affiliative and dominance network on the transfer entropy network. For this analysis, we calculated transfer entropy with a history length of 1. We calculated transfer entropies using the "RTransferEntropy" (Behrendt et al., 2019) package in R.

Although transfer entropy provides a suitable relative measure of the longer-term influence that individuals have over the sleep states of their group-mates, it offers little insight into the role of collective dynamics in individual waking events during the night, as its calculation requires probability distributions of the data aggregated over time. Thus, to gain a better understanding of how the collective dynamics of nocturnal awakenings are shaped by the relationships between group members and the importance of these social influences on sleep patterns, we performed a network-based diffusion analysis (NBDA; Franz & Nunn, 2009; Hasenjager et al., 2021; Hoppitt et al., 2010). NBDA assesses the role of the social network in guiding the spread of a target trait through a population. The importance of social processes in trait acquisition is indicated by the extent to which the trait follows the connections of the network as it diffuses throughout the population, or, alternatively, spreads randomly with respect to the network. Originally developed to investigate social learning, whereby the acquired trait represents a learned behavior, NBDA was applied in our study to analyze the spread of wakefulness during the night. Here, the transition from sleep to waking represents acquisition of the target trait.

We adapted the "time of acquisition diffusion analysis" (TADA) variant of NBDA to assess the spread of wakefulness via the study group's affiliative and relative dominance networks. Because NBDA in its original form assumes that individuals cannot lose a trait after acquiring it, we applied a custom implementation that modelled all trait acquisitions (i.e. waking events) of each individual, regardless of whether the individual was waking for the first time or had previously woken and fallen back asleep. In conjunction with a specification of the duration for which individuals remained awake after waking, this adaptation allowed us to implement NBDA for our use-case.

In addition to modelling the role of the social network(s) in trait acquisition, our implementation of NBDA also modelled the influence of individual-level variables (ILVs) on the probability of waking either asocially (i.e. independent of the diffusion of wakefulness through the affiliative and relative dominance networks) or socially (i.e. as a result of the diffusion of wakefulness

through the affiliative and relative dominance networks). Therefore, we also included the age and sex of each individual as variables in the analysis alongside the group's affiliative and relative dominance network. The strength of the social influences on waking, estimated through the parameters *s1* (affiliative network) and *s2* (relative dominance network), is estimated relative to the baseline rate of waking. To ensure a stable parameterization of the models, we set the baseline rate of waking to the midpoint of all ILVs.

We ran a model for each possible combination of parameters, including with and without one or both of the affiliative and relative dominance networks, such that some models evaluated nighttime waking as a completely asocial process. Because we ran "unconstrained" models (Hasenjager et al., 2021) that estimated a separate parameter for the influence of each ILV on social waking and asocial waking (Hasenjager et al., 2021; Laland & Hoppitt, 2013), all parameter combinations resulted in a total of 200 models. After running the models, we calculated model support using AICc (Burnham & Anderson, 2002) and summed the Akaike weights for each variable across models to assess the support for each variable. This procedure enabled us to determine the support for each social network (affiliative and relative dominance) in contributing to the pattern of waking across the group throughout the night, as well as the support for the influence of each ILV on both the probability of waking socially and the probability of waking asocially. We considered variables that received summed Akaike weights of greater than 0.5 to be influential.

We measured the strength of influence of each social network on nocturnal awakening by using the best performing model to estimate the percentage of waking events that resulted from the social transmission of wakefulness through the respective networks. We calculated 95% confidence intervals as 1.96 times the standard error of these percentages extracted from the best performing model. For the ILVs deemed to be influential, we estimated the effect sizes by calculating the weighted medians of their effect sizes across all models, as weighted means can be biased by extreme values (Hasenjager et al., 2021). We calculated 95% confidence intervals as 1.96 times the standard error of the respective effect sizes in the best performing model.

We ran two sets of complete models and evaluated them as described above to account for uncertainty in the order of waking of individuals that awoke within the same minute. Given the

minute resolution of our sleep-wake classification, it was probable that waking events that appeared simultaneous in our data were not actually simultaneous. However, our implementation of TADA considered social transmission to be impossible between two simultaneous waking events. Thus, we ran two types of models. First, we ran a set of conservative models that assumed that waking events that occurred within the same minute were "tied," such that there was no possibility of these waking events having a social influence on each other. These conservative models likely underestimated the transmission of wakefulness through the social networks. Second, we ran a set of models that assumed a random order of the waking events that occurred within the same minute. These models allowed for the possibility that waking events that occurred first (according to the randomized order) could have precipitated the subsequent waking of group-mates within the same minute. We repeated this second set of models five times, each with a different randomized order of waking events that occurred within the same minute. We refer to these models in the results tables (Table S2.3, S2.4) as "not tied." We focused our presentation of the results on the "tied" models to remain conservative in our interpretation. For all NBDA analyses, we used data from 21:00 to 05:00 prior to August 10, 2019.

We tested the influence of the group's spatial network configuration on a given night on the total time each individual spent sleeping that night to develop insights into the mechanism by which wakefulness transmits socially during the night. We predicted that if the social transmission of wakefulness occurs via the spatial network, with individuals woken by the waking activity of any nearby group-mates, then individuals would sleep least on nights during which the entire group slept within a spatially confined area. Conversely, we predicted that a spatial network with low density and high modularity would facilitate longer total sleep time, as a lower density network would decrease the opportunity for waking activity to propagate to nearby individuals and higher modularity of the network would ensure that wakefulness that does propagate is contained within a small cluster of individuals. To test these predictions, we extracted the spatial network of the group on each night at 22:00 from the detection positions in the infrared imagery (see *Extracting nighttime spatial positioning and individual movement from infrared imagery*). We considered individuals within three meters of each other to be connected within the spatial network and used the "igraph" package (Csardi & Nepusz, 2005) in R to measure the density and modularity of the network. In the calculation of

modularity, we assigned community membership with the walktrap clustering algorithm (Pons & Latapy, 2005). We modelled individuals' total time spent sleeping from 18:00 to 06:30 with a Bayesian linear mixed model (LMM) with fixed effects for spatial network density, spatial network modularity, age, and sex. We included random intercepts for individual and night identity. This analysis was limited to the nights on which we collected infrared recordings until at least 22:00 (Table S2.2).

We leveraged the tracking data from the infrared imagery to investigate the possibility that wakefulness propagates throughout the group not as a result of active individuals waking proximal group-mates where the active individuals awoke, but, rather, as a result of these individuals waking nearby group-mates upon relocating within the sleep site. We spatially discretized the movement of the infrared tracks at one-meter resolution and extracted discrete relocations of individuals within the sleep site as instances in which an individual exceeded the one-meter threshold from its previous spatially discretized location for the first time in five minutes. We considered the discrete relocation to begin when the individual most recently started moving (according to the stationary vs. non-stationary classification) prior to exceeding the one-meter threshold and to end when the individual stopped moving following the last time it exceeded the threshold and prior to five minutes of not exceeding the threshold. We then recorded the number of individuals that subsequently (in the following minute) transitioned from stationary behavior to non-stationary behavior within a one-meter radius of the individual's location when it commenced its discrete relocation, when it ended the relocation, and every time it exceeded the one-meter spatial discretization threshold (i.e. made a non-local movement step) during its relocation. We assumed that the focal individual's activity led to the transitions of these group-mates from stationary to non-stationary behaviors, and we note that each transition from stationary to non-stationary behavior could be attributed to a maximum of one focal individual. We then used a two-sided paired Wilcoxon signed rank test to test whether relocating individuals caused more group-mates to transition from stationary to non-stationary behavior after moving away from their initial position than at the position where they commenced relocation. We note that although individuals actively moving must be awake, individuals that are not moving are not necessarily asleep, and so we cannot assess sleep state by the automated detection of the movement of

individuals in the infrared imagery. Thus, this analysis tested whether an individual was more likely to cause nearby group-mates to become active, not necessarily to awaken, in proximity to the location where the individual first became active or, rather, upon relocating away from that location. For more details on the algorithm, see the pseudo-code in Fig. S2.10. For this analysis, we used the tracks that had been manually corrected and trimmed them to the period between 20:00 to 05:00, instead of 21:00 to 05:00, so that we could augment limited sample size of the manually corrected tracks. Although 20:00 is a less conservative start time for the analysis than 21:00, it is still within the sleep period of wild baboons within this population (Loftus et al., 2022).

Lastly, we explored the consequences of the collective dynamics during the sleep period on individuals' ability to meet their physiological sleep requirements by testing the effect of an individual's position within the group's social networks on total time spent sleeping. We modelled the total time spent sleeping from 18:00 to 06:30 with a Bayesian LMM as a function of age, sex, dominance, and centrality in the affiliative network. We included random intercepts for individual and night identity. We calculated dominance as an individual's out-strength (weighted out-degree) minus its in-strength (weighted in-degree) in the absolute dominance network. We calculated centrality using the "igraph" package (Csardi & Nepusz, 2005) in R to calculate eigenvector centrality in the affiliative network.

We ran all Bayesian models with the R package "brms" (Bürkner, 2017). We used diffuse, mean-zero Gaussian priors for all fixed effects variables. The default priors in "brms" were used for the intercept, as well as all random effects variables. Model estimates are generated from four Hamiltonian Monte Carlo chains, each with 2500 burn-in iterations and 2500 sampling iterations. Trace plots indicated sufficient mixing and convergence of the four chains on the same posterior region. We ran all models with response and predictor variables standardized. Model estimates reported in the main text in the form Estimate [lower CI, upper CI] reflect the mean of the posterior distribution followed by the lower and upper 95% credible interval bounds of the standardized models. Model estimates reported in the text in any other form, as well as plots generated from model estimates, were back-transformed from standardized model estimates. Model output tables and plots from the posterior predictive checks are included in the Supplemental Materials.

Data availability

GPS and accelerometry data generated during this study are stored in the Movebank data repository (www.movebank.org) under the project name “Papio Anubis Mpala 2019”. For permission and access to download the data from Movebank, please contact Meg Crofoot (mcrofoot@ab.mpg.de). The raw infrared imaging data are archived on the storage server for the Department for the Ecology of Animal Societies in the Max Planck Institute of Animal Behavior, with a backup at the Max Planck Computing and Data Facility in Garching, Germany. The raw infrared imaging data is contained within the following directory of the storage server: “/EAS_shared/baboon/archive/rawdata/video/thermal/2019_summer/cliff_data/thermal/viewpoint_1/T1020/”. All other data necessary to reproduce the analyses are archived on the same server in the following directory: “EAS_shared/baboon/archive/pubs/Loftus_dissertation/social_sleep/”. For access to data archived on the storage server for the Department for the Ecology of Animal Societies, please contact Meg Crofoot (mcrofoot@ab.mpg.de). All code and instructions necessary to reproduce the final results from the raw data are published on GitHub (https://github.com/CarterLoftus/social_sleep/) and archived on Zenodo (https://doi.org/10.5281/zenodo.6913229).

Supplemental Materials

Collar ID	Sex	Age	Weight (kg)	Battery size	Capture date	ACC start date	ACC end date
2428	M	A	25	D	2019-07-18	2019-07-19	2019-08-17
2433	F	A	15.5	D	2019-07-17	2019-07-19	2019-08-17
2434	F	A	16	D	2019-07-17	2019-07-19	2019-08-18
2436	F	J	13	D	2019-07-17	2019-07-19	2019-08-17
2441	F	SA	12	D	2019-07-18	2019-07-19	2019-08-17
2447	F	SA	14	D	2019-07-17	2019-07-19	2019-08-18
2448	F	J	11	D	2019-07-17	NA	NA
2450	F	SA	14	D	2019-07-18	2019-07-19	2019-08-04
2451	M	A	28	D	2019-07-18	2019-07-19	2019-08-03
2454	M	A	25.5	D	2019-07-18	2019-07-19	2019-08-18
2455	M	J	8	C	2019-07-17	2019-07-19	2019-07-25
6890	F	SA	9	C	2019-07-15	2019-07-19	2019-08-18
6891	M	J	11	C	2019-07-15	2019-07-19	2019-07-29
6892	F	SA	11	C	2019-07-15	2019-07-19	2019-08-18
6894	M	J	9	C	2019-07-15	2019-07-19	2019-07-27
6897	F	A	13.5	C	2019-07-15	2019-07-19	2019-08-10
6898	F	J	8	C	2019-07-15	2019-07-19	2019-08-01

6900	F	SA	16	C	2019-07-15	2019-07-19	2019-08-18
6910	M	A	28.5	D	2019-07-17	2019-07-19	2019-08-18
6914	F	SA	13.5	D	2019-07-17	2019-07-19	2019-07-23
6915	M	SA	20.5	D	2019-07-15	2019-07-19	2019-08-15
6921	M	SA	17	D	2019-07-17	2019-07-19	2019-08-18
6924	F	SA	15.5	D	2019-07-17	2019-07-19	2019-08-17
6927	M	A	24	D	2019-07-15	2019-07-19	2019-08-18
6932	M	A	28.5	D	2019-07-17	2019-07-19	2019-08-18
6933	M	SA	17	D	2019-07-15	2019-07-19	2019-08-18
6934	M	SA	15	C	2019-07-15	2019-07-19	2019-08-12

Table S2.1. Individual metadata. Table contains the identity, sex, age, weight, battery size of the GPS/accelerometry collar, and capture date, as well as the start and end dates of accelerometry data collection for each collared individual. F = female, M = male, A = adult, SA = subadult, J = juvenile, C = C cell battery, D = D cell battery, ACC = accelerometry. Note that ID 2448's collar failed to collect any data.

Night	Recording start time	Recording end time	Duration (hours)
2019-07-31	2019-07-31 18:00:09	2019-08-01 02:38:35	8.64
2019-08-01	2019-08-01 17:06:02	2019-08-02 06:47:33	13.69
2019-08-02	2019-08-02 16:05:07	2019-08-02 21:18:08	5.22
2019-08-03	2019-08-03 16:30:06	2019-08-04 04:57:38	12.46
2019-08-04	2019-08-04 16:30:09	2019-08-05 04:11:11	11.68
2019-08-06	2019-08-06 16:20:05	2019-08-06 21:32:18	5.2
2019-08-07	2019-08-07 17:00:05	2019-08-08 06:56:25	13.94
2019-08-08	2019-08-08 16:30:05	2019-08-09 03:10:39	10.68
2019-08-09	2019-08-09 16:30:08	2019-08-09 21:34:24	5.07
2019-08-10	2019-08-10 16:30:03	2019-08-10 18:27:12	1.95
2019-08-11	2019-08-11 16:30:06	2019-08-12 00:31:23	8.02
2019-08-12	2019-08-12 16:56:03	2019-08-12 21:32:09	4.6
2019-08-13	2019-08-13 16:30:06	2019-08-13 19:42:38	3.21
2019-08-14	2019-08-14 17:00:05	2019-08-14 23:09:47	6.16
2019-08-15	2019-08-15 16:35:05	2019-08-15 21:51:29	5.27
2019-08-16	2019-08-16 16:30:06	2019-08-17 00:15:25	7.76
2019-08-17	2019-08-17 17:00:02	2019-08-17 22:19:22	5.32
2019-08-18	2019-08-18 17:11:02	2019-08-18 18:51:57	1.68
2019-08-19	2019-08-19 16:20:01	2019-08-19 20:37:34	4.29
2019-08-20	2019-08-20 16:23:03	2019-08-21 03:01:46	10.65
2019-08-21	2019-08-21 16:01:01	2019-08-22 01:15:20	9.24

Table S2.2. Infrared recording metadata. Table depicts the dates on which infrared imagery was collected, as well as the start and end times of recording, and the total duration of the recording (in hours). Note that the night column indicates the date of recording start (e.g. night 2019-08-01 starts on 2019-08-01 and ends on 2019-08-02).

Diffusion	Support for affiliative network social models (summed Akaike weights)	% of events through affiliative network social transmission	95% confidence intervals	Support for dominance network social model (summed Akaike weights)	% of events through dominance network social transmission	95% confidence intervals
Tied	1.000	10.65	9.10-12.00	1.000	4.40	2.84-5.70
Not tied 1	1.000	17.93	16.37-19.41	0.969	2.25	0.71-3.66
Not tied 2	1.000	17.13	15.62-18.58	1.000	3.73	2.12-5.18
Not tied 3	1.000	17.16	15.68-18.58	0.999	3.33	1.73-4.79
Not tied 4	1.000	17.30	15.60-18.82	0.996	2.81	1.25-4.25
Not tied 5	1.000	17.53	15.83-19.11	0.952	2.31	0.75-3.77

Table S2.3. Support for (as indicated by summed Akaike weights) and strength of social transmission in network-based diffusion analysis (NBDA).

		Diffusion	Sex	Age (adult/other)	Age (juv./other)
Influence on asocial learning	Support	Tied	**0.883**	**1.000**	0.458
		Not tied 1	**0.914**	**1.000**	0.301
		Not tied 2	**0.605**	**1.000**	0.303
		Not tied 3	**0.782**	**1.000**	0.307
		Not tied 4	**0.702**	**1.000**	0.336
		Not tied 5	**0.945**	**1.000**	0.362

	Effect size	Tied	Males 1.08 [1.01-1.15] times more likely to wake up asocially compared to females	Adults 1.28 [1.20-1.37] times more likely to wake up asocially compared to other age classes	-
		Not tied 1	1.08 [1.02-1.16]	1.29 [1.21-1.38]	-
		Not tied 2	1.06 [0.99-1.13]	1.24 [1.18-1.31]	-
		Not tied 3	1.07 [1.00-1.14]	1.24 [1.18-1.31]	-
		Not tied 4	1.06 [0.99-1.13]	1.26 [1.19-1.33]	-
		Not tied 5	1.09 [1.02-1.16]	1.24 [1.18-1.31]	-
Influence on social learning	Support	Tied	**0.663**	**0.985**	**0.918**
		Not tied 1	**0.645**	**0.733**	0.384
		Not tied 2	**0.966**	0.277	**0.582**
		Not tied 3	**0.837**	0.417	**0.545**
		Not tied 4	**0.897**	0.471	0.302
		Not tied 5	**0.548**	0.361	0.287
	Effect size	Tied	Males 1.25 [0.97-1.62] times more likely to wake up socially compared to females	Adults 0.60 [0.43-0.83] times as likely to wake up socially compared to other age classes	Juveniles 0.67 [0.48-0.93] times as likely to wake up socially compared to other age classes
		Not tied 1	1.20 [0.98-1.46]	0.80 [0.64-1.00]	-
		Not tied 2	1.33 [1.10-1.62]	-	0.82 [0.64-1.05]
		Not tied 3	1.25 [1.02-1.52]	-	0.85 [0.66-1.08]
		Not tied 4	1.29 [1.06-1.57]	-	-

		Not tied 5	1.15 [0.94-1.40]	-	-

Table S2.4. Support for (as indicated by summed Akaike weights) individual-level variables (ILVs), including parameter estimates and 95% confidence intervals, from NBDA. Bolded figures correspond to variables that were deemed influential by the models (received greater than 0.5 summed Akaike weights). Note that we only report estimates and confidence intervals for variables that were deemed influential.

		Behavioral scoring		
		Awake		Asleep
		Wakefulness	Resting wakefulness	Sleep
Accelerometer-based sleep classification	Awake	16	93	5
	Asleep	4	163	369

Table S2.5. Confusion matrix reporting the performance of the accelerometer-based sleep classification algorithm. Table entries represent the number of minute-epochs classified according to the accelerometer-based algorithm and direct behavioral observation, with the direct behavioral observations taken to be ground-truth.

		Behavioral scoring	
		Non-stationary	Stationary
Classification from XGBoost model	Non-stationary	36	2
	Stationary	6	2550

Table S2.6. Confusion matrix reporting the performance of the decision-tree machine-learning model with extreme gradient boosting (XGBoost model) used to classify the behavior of individuals in the infrared imagery as either stationary or non-stationary. Table entries represent the number of second-epochs classified according to the XGBoost model and direct behavioral observation, with the direct behavioral observations taken to be ground-truth.

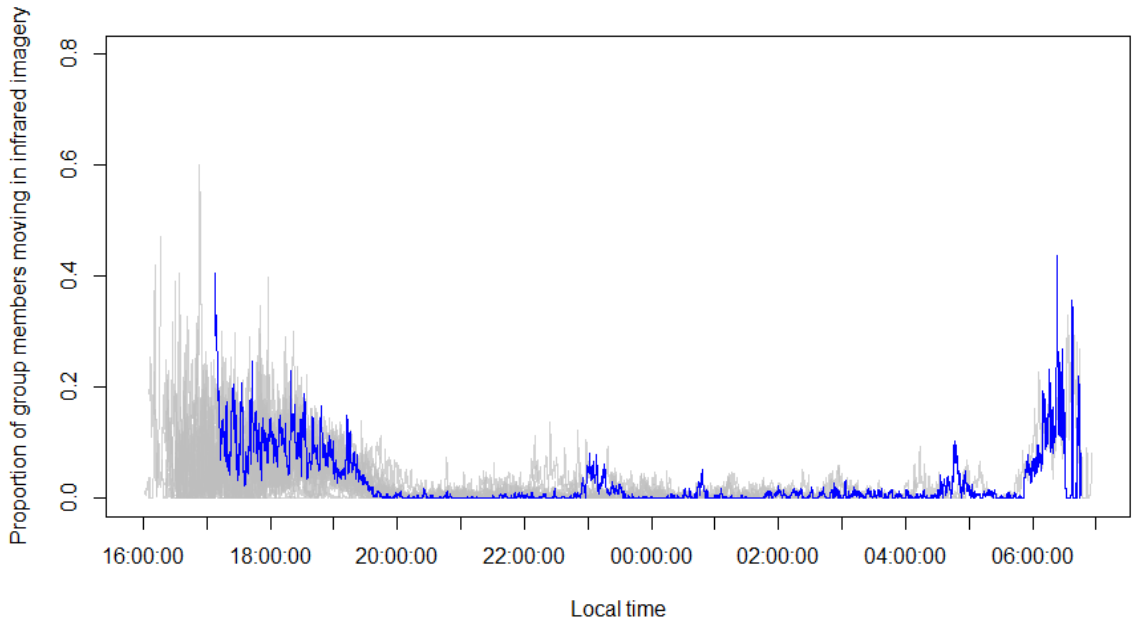

Figure S2.1. The proportion of group members exhibiting non-stationary behavior in the infrared imagery (as determined by predictions from the extreme gradient boosted decision-tree machine-learning model on the uncorrected tracks) as a function of time of day. The proportion of group members moving was smoothed with a moving mean with a 1-minute time window before plotting. A separate semi-transparent grey line is plotted for each individual night of data collection. One particular night, 2019-08-01, is highlighted in blue as an example.

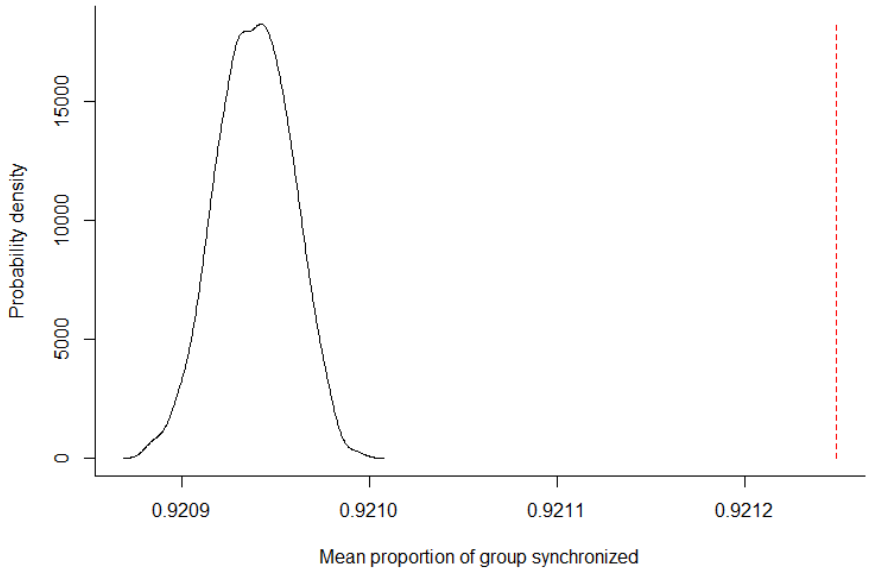

Figure S2.2. There was a higher mean proportion of group that was synchronized in their sleep vs. wake state during the night over the study period (dotted red line) than expected based on 1000 time-shifted datasets (black distribution).

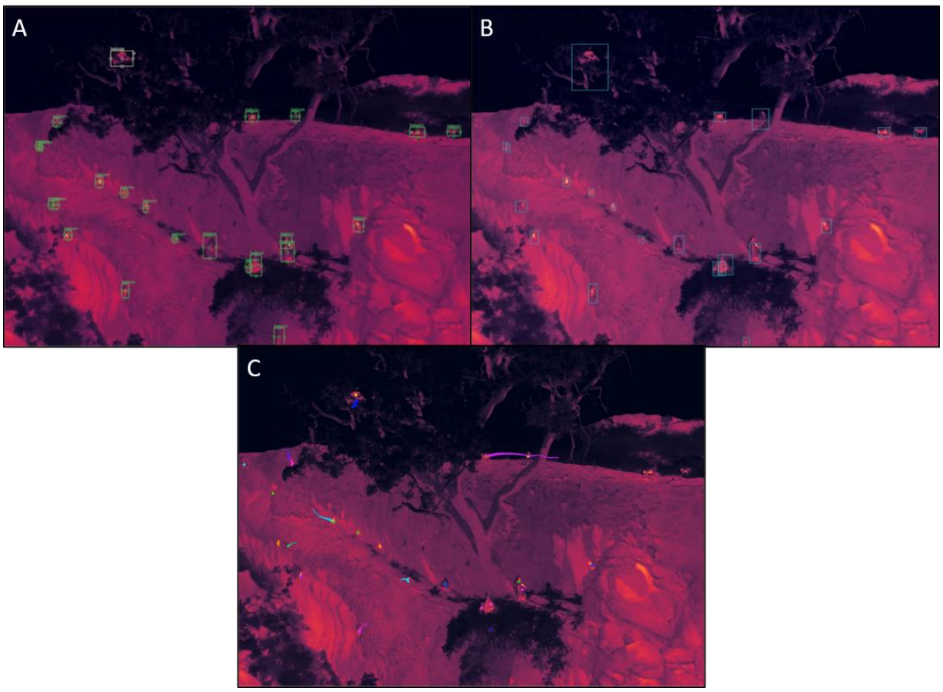

Figure S2.3. Depiction of the workflow to obtain tracks from the infrared imagery. We first annotated all baboons visible in 976 frames distributed across the study period in the commercial software Loopy (Loopbio GmbH, Austria; A: green bounding boxes were drawn around each baboon by an observer). These annotations were used to train a convolutional neural network (CNN) that automatically detected baboons in the infrared imagery (B: blue bounding boxes reflect CNN predictions). The center points of these detections were knit together across frames to create individual trajectories using a modification of the Hungarian algorithm (Kuhn, 1955; C). These trajectories were then manually corrected by a human observer.

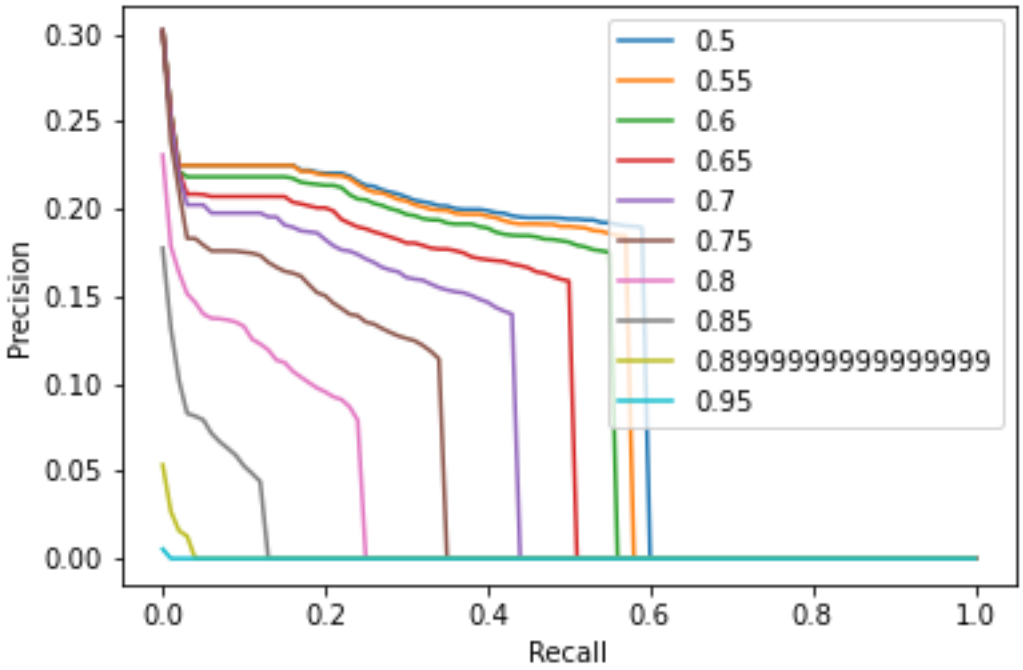

Figure S2.4. Precision-recall curve of CNN used to predict the locations of baboons, which were then used to measure attributes of the group's spatial network during the night (score threshold = 0.60).

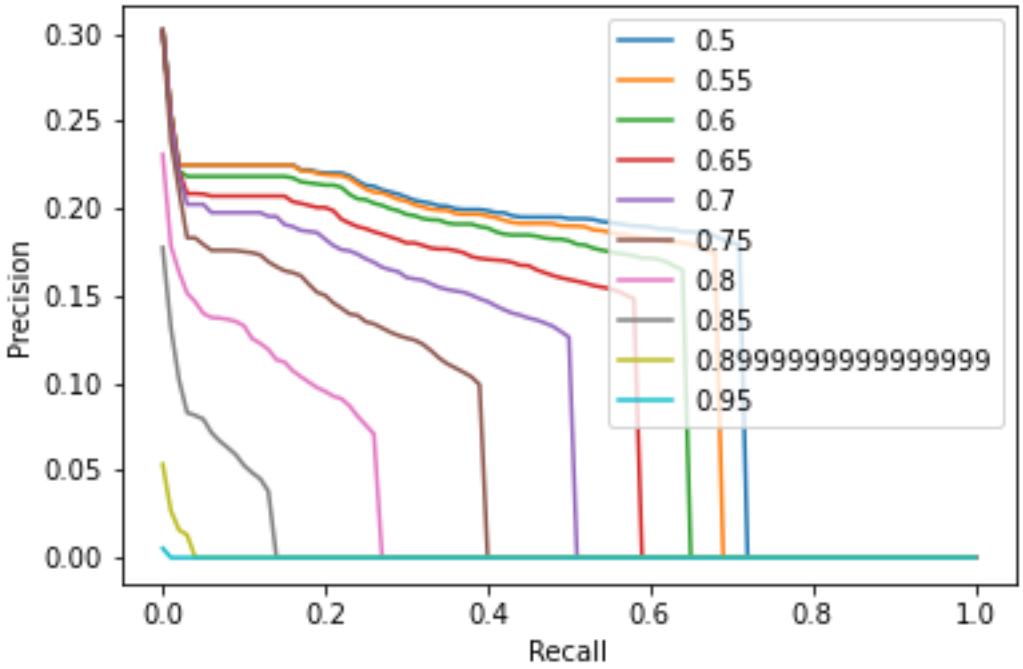

Figure S2.5. Precision-recall curve of CNN used to predict the locations of baboons, which were then used to generate individual tracks for each baboon (score threshold = 0.80).

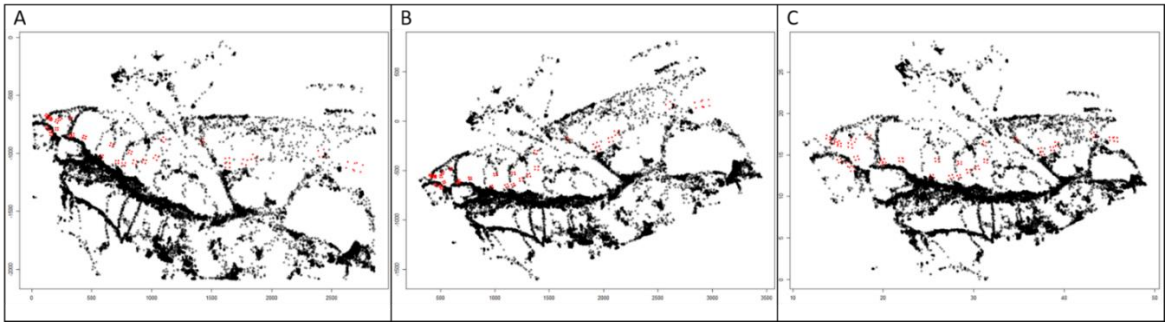

Figure S2.6. Depiction of the spatial calibration applied to the location data from the infrared imagery. (A) represents the original, unmanipulated data, with black points indicating the coordinates of all tracks produced from one night of data collection (downsampled by a factor of 10 for plotting), and red points indicating the coordinates of the four corners of the measurement object at several time points as it was moved across the camera field-of-view. (B) represents the same coordinates as in (A), after the rotation matrix was applied to them. We then applied the spatial correction to all coordinates in (B) to obtain (C).

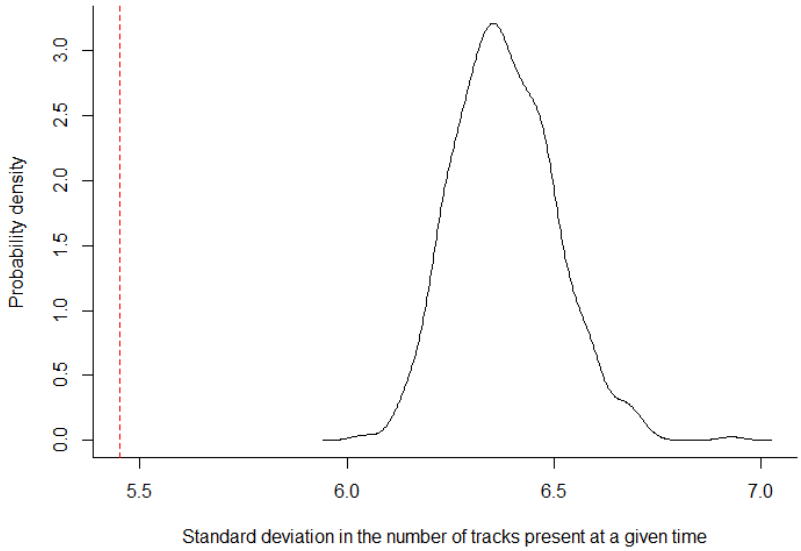

Figure S2.7. The lower standard deviation in the number of tracks present in the infrared imagery at any given time in the empirical data (dotted red line) compared to those from 1000 time-shifted datasets (black distribution) suggests that tracks were not synchronized in their presence more than we would expect by chance (actually, the opposite was true: tracks were staggered in their presence), and thus, any result indicating synchronized movement of the tracks would not be a spurious one.

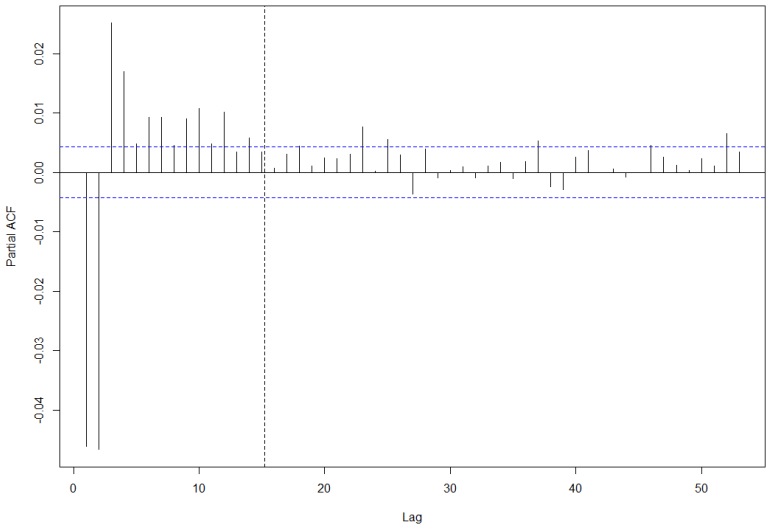

Figure S2.8. Partial autocorrelation plot of the transition from sleep to waking during the night, limited to the data that fit the criteria to be included in the model of the probability of a baboon waking as a function of the number of group-mates that awoke in the previous minute. The dotted line, drawn at lag 15, indicates the lag where we considered the autocorrelation to have dissipated. We therefore downsampled the data, by keeping only every 15th data point, before modeling the probability of a baboon waking based on the number of its group-mates that awoke in the previous minute.

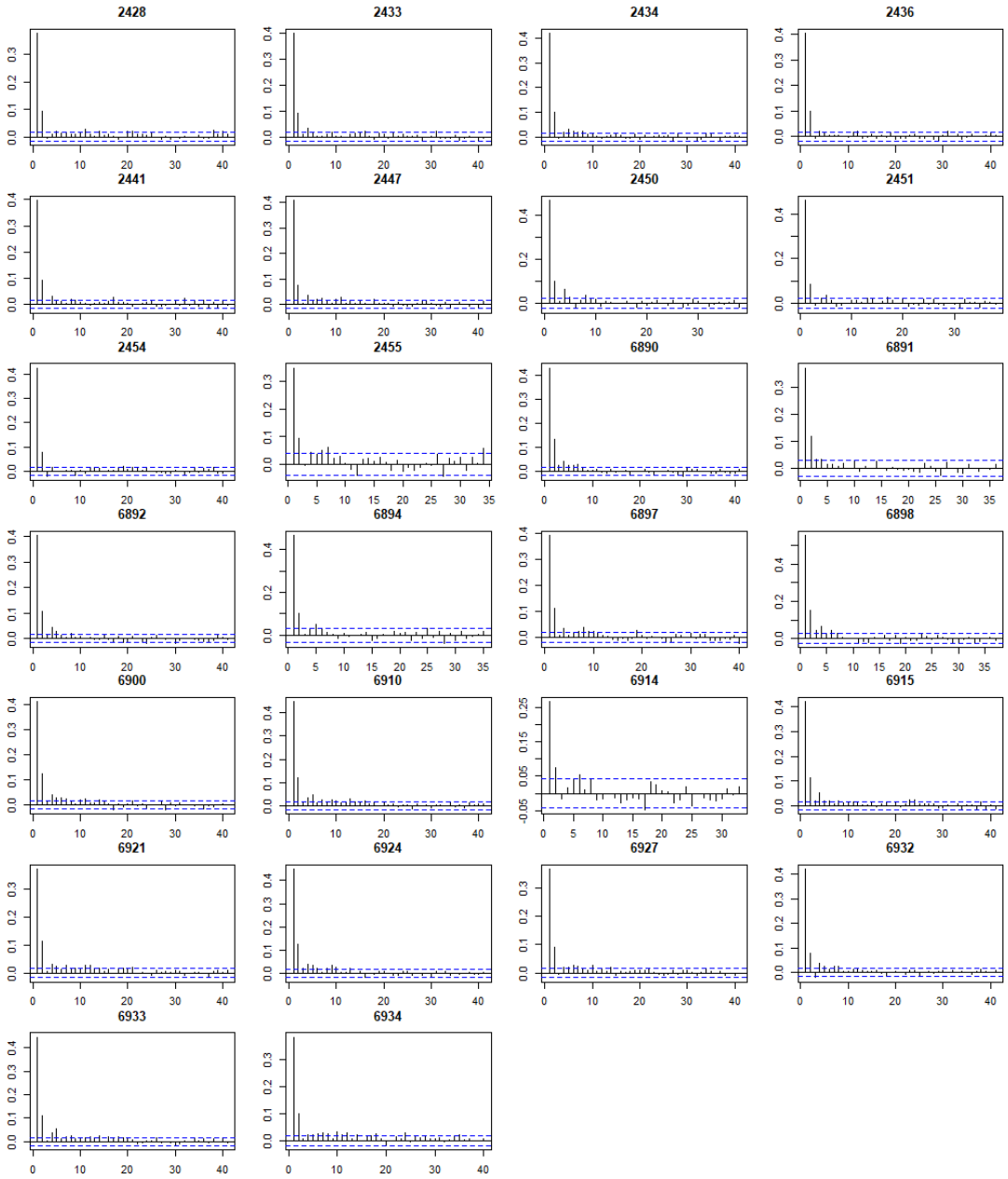

Figure S2.9. Partial autocorrelation plots of sleep state during the period from 21:00 to 05:00 for each individual. The autocorrelation appears to dissipate at lag three, which informed our use of the history length of three for the transfer entropy analysis.

Spatial discretization

- For each night of data:
    - For each track:
        - Set the tracks initial location to be its initial "spatially discretized" location
        - For each location recorded:
            - Measure the distance to the previous spatially discretized location recorded
                - If this distance is greater than the spatial discretization threshold (1 meter), record this location as the current spatially discretized location
                - If the distance is not greater than the spatial discretization threshold, record the previous spatially discretized location as the current spatially discretized location

Do focal individuals cause group-mates to become active where the focal individuals initially became active themselves, or after relocating within the sleep site?

- For each night of data:
    - Trim the tracking data to 20:00 – 05:00
    - Create a dataframe of each discrete transition from stationary to non-stationary (discrete = separated by a one-minute period of stationary behavior)
        - If an individual exhibits non-stationary behavior before a one-minute period of stationary behavior, consider the first instance of non-stationary behavior a discrete transition from stationary to non-stationary behavior
    - Create a dataframe of each discrete relocation (discrete relocation = period in which individuals show movement (i.e. non-zero step length) according to their spatially discretized location, separated by periods of 5 minutes of no movement in their spatially discretized location)
        - If an individual exhibits movement according to their spatially discretized locations before a period of 5 minutes of no movement according to their spatially discretized locations, consider the first instance of spatially discretized movement to be the beginning of a relocation
        - Set the start time of the relocation event to be the time at which the individual most recently transitioned from stationary to non-stationary behavor (following 10 seconds of non-stationary behavior) within the previous minute prior to the first non-zero step length in the spatially discretized locations of the relocation event
            - If the individual did not transition from stationary to non-staionary behavior within the previous minute, remove this relocation event from the dataframe
        - Set the end time of the relocation to be the soonest transition from non-stationary behavior to stationary behavior (preceding 10 seconds of stationary behavior) within the minute following the last non-zero step length in the spatially discretized locations of the relocation event

- If the individual did not transition from non-stationary to stationary behavior within this following minute, set the end of the relocation event to be the time of the last non-zero step length in the spatially discretized locations

- Order the relocation events by their start times
- For each relocation event (in order of start time):
    - Subset the tracking data to the data of the individual who relocated and to the time of the relocation (after it starts and before it ends)
    - Extract and save the number of individuals within one meter of the location where there this relocation event began that transitioned from stationary to non-stationary behavior within one minute following the beginning of the relocation event. This represents the number of individuals that transitioned from stationary to non-stationary behavior where the relocating individual began the relocation
    - Remove the corresponding transitions from the data frame indicating when individuals transitioned from stationary to non-stationary, so that this transition cannot be attributed to more than one relocating individual
    - For each time that the relocating baboon moves greater than one meter, according to its spatially discretized location, as well as for its last location during the relocation event:
        - Extract the number of individuals within one meter of the relocating baboon' current location that transitioned from stationary to non-stationary behavior within one minute following this timestamp. Add this to a cumulative total indicating the number of baboons that transitioned from stationary to non-stationary behavior after the relocating baboon moved away from its original position
        - Remove the corresponding transitions from the data frame indicating when individuals transitioned from stationary to non-stationary behavior, so that this transition cannot be attributed to more than one relocating individual

- Concatenate the data from all relocations on all nights and perform a two-sided paired Wilcoxen signed rank test comparing the number of individuals that transitioned from stationary to non-stationary behavior where a relocating baboon first began its relocation to the number of individuals that transitioned from stationary to non-stationary behavior in proximity to where the baboon then traveled during its relocation (after leaving its original position)

Figure S2.10. Pseudo-code for the algorithm to determine whether individuals actively relocating during the night caused more group-mates to become active where they began their relocation or after relocating within the sleep site.

Model outputs and fit

	Probability of waking	
Predictors	*Odds Ratios*	*CI (95%)*
Intercept	0.04	0.04 – 0.05
Number of individual awakening in previous minute	1.10	1.02 – 1.18
Time since start of night (spline, b)	1.14	0.16 – 4.84
Time since start of night (spline, sd)	1.30	1.01 – 4.22
Random Effects		
σ^2	0.00	
τ_{00}	0.04	
ICC	0.01	
N_{night}	22	
N_{tag}	26	
Observations	14089	
Marginal R^2 / Conditional R^2	0.001 / 0.002	

Table S2.7. Model output table of the model of the probability of waking as a function of the number of group-mates that awoke in the previous minute.

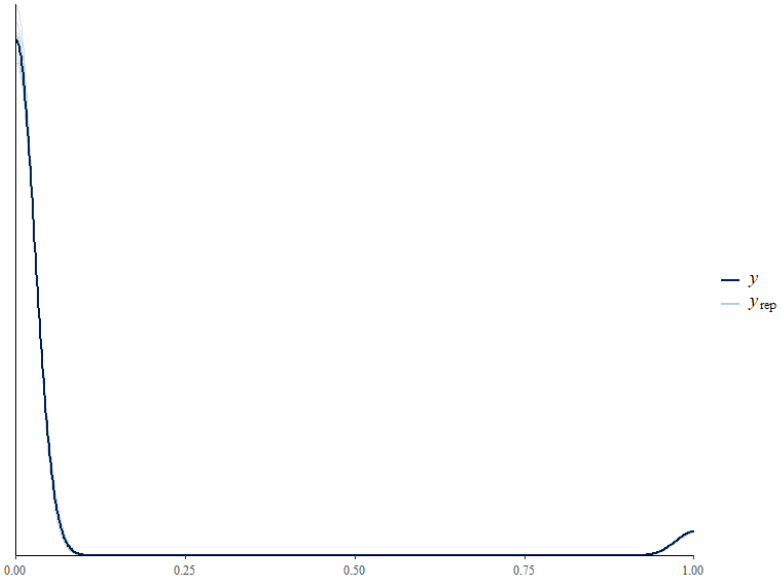

Figure S2.11. Posterior predictive check of the model of the probability of waking as a function of the number of group-mates that awoke in the previous minute.

Transfer entropy (standardized)

Predictors	*Estimates*	*CI (95%)*
Intercept	-0.04	-0.18 – 0.10
Affiliative score (standardized)	0.11	0.03 – 0.20
Dominance score (standardized)	0.07	-0.01 – 0.16
Random Effects		
σ^2	0.84	
$\tau_{00\ dy\_name}$	0.05	
$\tau_{00\ tag\_a}$	0.06	
$\tau_{00\ tag\_b}$	0.03	
ICC	0.15	
N_{tag_a}	26	
N_{tag_b}	26	
N_{dy_name}	325	
Observations	650	
Marginal R^2 / Conditional R^2	0.029 / 0.189	

Table S2.8. Model output table of the model of the transfer entropy between two individual's sleep states as a function of affiliative and dominance relationships.

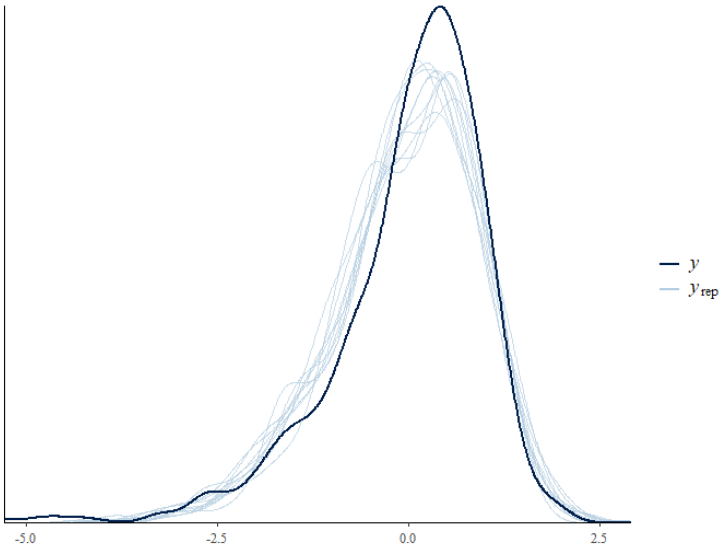

Figure S2.12. Posterior predictive check of the model of the transfer entropy between two individual's sleep states as a function of affiliative and dominance relationships.

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.20	-0.32 – 0.70
Spatial proximity network density (standardized)	-0.33	-2.17 – 1.53
Spatial proximity network modularity (standardized)	-0.40	-2.22 – 1.49
Sex: Male	0.03	-0.30 – 0.36
Age: Juvenile	0.12	-0.59 – 0.84
Age: Subadult	-0.51	-0.85 – -0.18
Random Effects		

σ^2	0.77
$\tau_{00\ night}$	0.35
$\tau_{00\ tag}$	0.02
ICC	0.32
N_{night}	10
N_{tag}	22
Observations	165
Marginal R^2 / Conditional R^2	0.134 / 0.281

Table S2.9. Model output table of the model of the total time spent sleeping from 18:00 to 06:30, with measures of the group's nighttime spatial network (density and modularity) as predictors.

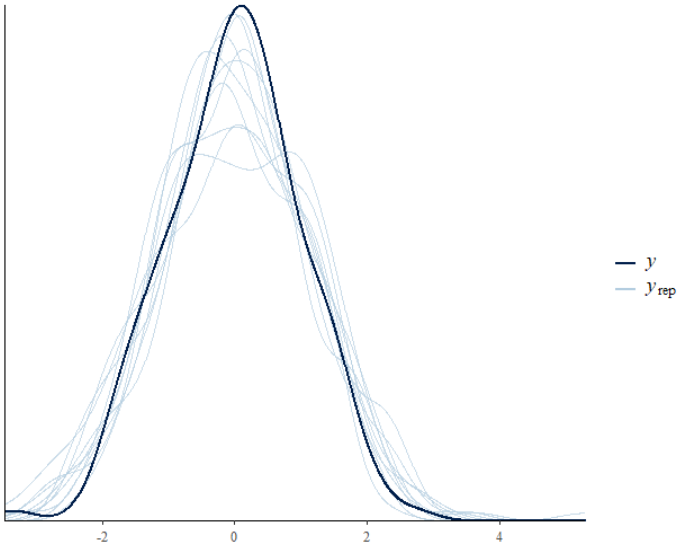

Figure S2.13. Posterior predictive check of the model of the total time spent sleeping from 18:00 to 06:30, with measures of the group's nighttime spatial network (density and modularity) as predictors.

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.08	-0.20 – 0.36
Eigenvector centrality in affiliative network (standardized)	-0.14	-0.24 – -0.04
Dominance (standardized)	0.01	-0.08 – 0.11
Sex: Male	-0.07	-0.25 – 0.12
Age: Juvenile	-0.33	-0.63 – -0.05
Age: Subadult	-0.16	-0.37 – 0.05
Random Effects		
σ^2	0.68	
$\tau_{00\ night}$	0.34	
$\tau_{00\ tag}$	0.01	
ICC	0.34	
N_{night}	30	
N_{tag}	26	

Observations	572
Marginal R^2 / Conditional R^2	0.042 / 0.335

Table S2.10. Model output table of the model of the total time spent sleeping from 18:00 to 06:30, with individual position within the group's social networks (affiliative and dominance) as predictors. Dominance is equal to an individual's in-strength subtracted from its out-strength in the absolute dominance network.

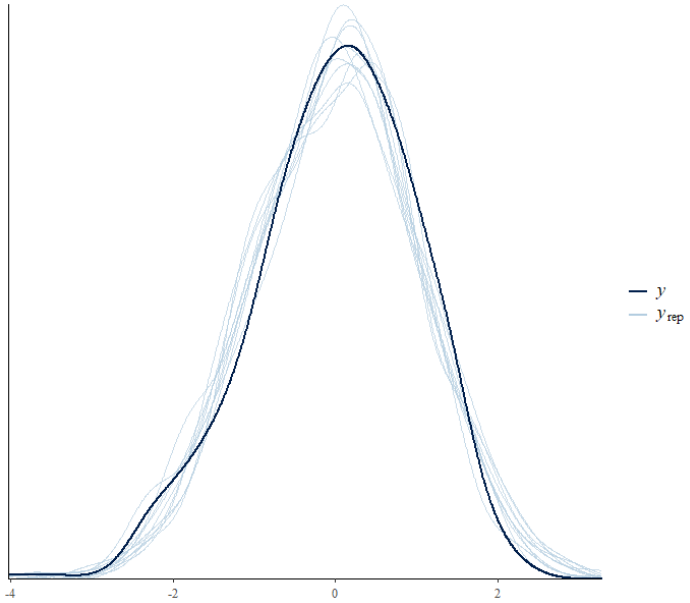

Figure S2.14. Posterior predictive check of the model of the total time spent sleeping from 18:00 to 06:30, with individual position within the group's social networks (affiliative and dominance) as predictors.

Chapter 3: The social dynamics of sleep catalyze tolerant relationships between baboon groups

Abstract

Sleep is essential for the health and survival of all animals. For many animals, sleep occurs in a social context, and the ability to obtain high-quality sleep may be fundamentally influenced by the behaviors of their neighbors. Because sleep research has primarily focused on lone individuals in laboratory settings, little is known about the social dynamics of sleep. To shed light on how the social environment both shapes, and is shaped by sleep patterns in the wild, we used GPS and tri-axial accelerometry over a one-year period to track the movements and sleep patterns of neighboring groups of wild olive baboons (*Papio anubis*). We found a strong interplay between social contexts and sleep dynamics. Members of neighboring groups exhibited lower quality sleep and greater temporal coordination in patterns of sleep and waking at night when their groups slept together compared to nights spent in lone groups. These social dynamics of sleep continued well beyond the sleep period: after sharing a sleep site, groups were substantially more likely to engage in extended associations that defined non-random attractions between groups across the study period. Thus, although social interactions during the sleep period jeopardize high-quality sleep, they may play an important role in catalyzing tolerant relationships between baboon groups. Our results reveal the trade-offs that animals face when sleeping amidst a social environment, and draw a link between the physiological need for sleep and the inter-group relationships that represent the building blocks of multi-level societies like our own.

Introduction

All animals sleep (Cirelli & Tononi, 2008). The ubiquity of sleep across taxa is paralleled by its importance: sleep plays a central role in maintaining the central nervous system (Xie et al., 2013), supporting cognitive functioning (Walker, 2009), and enhancing immune defense (Irwin, 2019; reviewed in Smeltzer et al., 2022). Many animals reap these benefits of sleep while mitigating the risks that are inherent to this period of reduced responsiveness by congregating during the sleep period to gain the protection of a shared refuge, maximize collective vigilance, or dilute the risk of predation (Finkbeiner et al., 2012; Lima et al., 2005). Thus, for many animals, sleep is embedded in a

social context. In this social context, the choices and behaviors of nearby conspecifics may fundamentally influence an individual's ability to obtain the high-quality sleep that is critical to fitness.

Prompted by calls to transition the investigation of sleep from the laboratory to the ecologically and socially relevant contexts in which it evolved (Aulsebrook et al., 2016; Rattenborg et al., 2017; Reinhardt, 2020), recent studies have suggested that interactions within groups of social animals continue well into the sleep period, with consequences for sleep (Karamihalev et al., 2019; Loftus et al., 2022; Smeltzer et al., 2022). However, the social environment of sleep is not always limited to familiar group-mates: congregation during the sleep period can often represent the primary interaction between individuals of solitary species and between groups of social species (Mohanty et al., 2022; Snyder-Mackler et al., 2012). While exceptionally few studies have explored the influence of group-mates on sleep in a social group, none has examined the sleep consequences for group-living animals of temporary associations with members of other social groups during the sleep period, despite important contrasts between the social dynamics of familiar and unfamiliar individuals that may lead to quite different sleep outcomes (Mochida & Nishikawa, 2014).

The influence on sleep of the congregation of multiple social groups may have particular significance that extends beyond an individual's ability to obtain high-quality sleep. Because social animals have comparatively infrequent encounters with extra-group (vs. intra-group) individuals, interactions that occur within the sleep period during temporary associations may overwhelmingly contribute to shaping the overall relationships between social groups (Leu et al., 2011). Thus, the feedback between social dynamics and sleep may be bi-directional: while the presence of neighboring groups may influence sleep, sleep dynamics—characterized by the choices of individuals and groups about where and when to sleep, as well as how to sleep, behave, and interact during the sleep period—may critically shape the relationships between neighboring groups.

Significant logistical challenges have hindered investigation of the interplay between sleep and inter-group social dynamics. Polysomnography—the gold standard for measuring sleep—requires subdermally or inter-cranially implanted electrodes, which, despite exciting advances in the use of polysomnography in the wild (reviewed in Rattenborg et al., 2017), remains intractable for use on

many wild animals (Smeltzer et al., 2022). Moreover, battery life limitations of mobile polysomnography restrict recordings to relatively short time periods (e.g. 10 days (Rattenborg et al., 2016), 8-10 days (Voirin et al., 2014)), which presents challenges to testing the influence of relatively infrequent events, such as inter-group encounters, on sleep behavior. Lastly, understanding how sleep patterns and behavior during the sleep period influence inter-group relationships involves monitoring not only sleep behavior, but also interactions between groups that may continue beyond, or occur entirely outside of, the sleep refuge—a daunting task that can involve the habituation and continuous observation of several groups of animals simultaneously.

Recent bio-logging approaches offer novel solutions to these historical challenges. Spurred by the dramatic rise in human wearable devices, accelerometry-based sleep classification has become an appealing, non-invasive alternative to polysomnography (Ancoli-Israel et al., 2003), and creates exciting opportunities to investigate the sleep of wild animals in new contexts and at dramatically longer time-scales (Watanabe & Rutz, 2022; Williams et al., 2021). Such methods can shed important light on the dynamics of sleep and social behavior, particularly in combination with simultaneously collected GPS data, which itself has opened new frontiers in the study of social behaviors from collective decision-making (Papageorgiou & Farine, 2020; Strandburg-Peshkin et al., 2015) to inter-group interactions (Markham et al., 2013).

Leveraging remotely-sensed accelerometry and GPS data, we monitored the sleep behavior of olive baboons (*Papio anubis*) to understand how the social environment both shapes, and is shaped by, sleep patterns. Baboons live in stable, multi-male, multi-female groups of 15-100 individuals, and neighboring groups have extensively overlapping home ranges (Altmann & Altmann, 1970; Isbell et al., 2018; Markham et al., 2013). Females are philopatric, remaining with their natal groups for life, while males disperse between groups (Altmann & Altmann, 1970; Cheney & Seyfarth, 2008). Although interactions between baboon groups can range from benign to aggressive, baboons are typically not considered to be highly tolerant of neighboring groups (Cheney & Seyfarth, 1977; Kitchen et al., 2004). At night, however, baboons seek refuge in trees and on rock outcroppings to avoid nocturnal predation from leopards, and due to the limited number of high-quality sleep sites on the landscape, neighboring groups occasionally spend the night in the same refuge (Bidner et al.,

2018; Markham et al., 2016). Although recent work has revealed that social and environmental pressures play a critical role in shaping the sleep of wild baboons (Loftus et al., 2022), we know nothing about how interactions between neighboring groups influence sleep, or how sleep dynamics, in turn, shape the social landscape across a baboon population.

We investigated the feedback loop between sleep and the social environment, by collecting accelerometry and GPS data from multiple individuals across four groups of wild olive baboons for over a year. Specifically, we examined how sharing a refuge with another group influenced the sleep quality of baboons, as well as their pattern of sleep and waking behavior during the night, using an algorithm that we have developed and validated for measuring sleep from accelerometry in baboons. By drawing upon simultaneous GPS data to identify and analyze encounters between groups both within and outside of the sleep site, we then tested how sleep dynamics feed back to influence subsequent inter-group interactions, and how these subsequent interactions scaled up to shape the relationships between baboon groups. Thus, combining accelerometry and GPS data collected from across a population provided a complete and objective account of both sleep patterns and interactions among study groups for the entire study duration, and, in doing so, offered a unique opportunity to explore inherent population-wide interdependences in sleep and space use.

Results

We collected GPS and accelerometry data from six adult females across four different groups of olive baboons ranging on Mpala Research Centre, in Laikipia, Kenya for over a year, resulting in 1644 baboon-days of data (Table S3.1). The home range of each study group, as indicated by the GPS data, partially overlapped with the home range of every other study group, and dyads with directly adjacent home ranges exhibited extensive overlap in their space use (Fig. 3.1, Tables S3.2, S3.3). Sleep sites were limited across the landscape, with all four groups combined sleeping in a total of 24 sleep sites during the entire data collection period. Extensive space use overlap, in conjunction with a limited number of available sleep sites, created a high potential for groups to make use of the same sleep sites as their neighbors over the course of the study, occasionally even on the same night. This potential was realized, as half of all sleep sites (12/24; Fig. 3.1) were used by more than one group

across the study period, and two groups spent the night together in the same sleep site on 46 different occasions.

The presence of another group at the sleep site influenced sleep patterns, with baboons experiencing lower quality sleep when sharing the sleep site with another group. By algorithmically identifying bouts of sleep from the accelerometry data, we found that baboons slept for 9.3 ± 0.02 hours (median ± SE) while at their sleep site. Individuals typically experienced sleep onset at 19:32 ± 2.4 minutes and waking at 05:55 ± 2.7 minutes. Within this sleep period, individuals exhibited a sleep efficiency of 81.4% ± 0.1% and a sleep fragmentation of 2.0 ± 0.02 awakenings per hour of sleep. However, when baboons shared their sleep site with another group, they slept for 33.5 minutes less, with 1.2% less efficiency and 0.15 more awakening per hour of sleep, on average, than when they slept with only their group-mates (Fig. 3.1; total sleep time hierarchical Bayesian regression (Student-t): standardized estimate [90% credible interval lower bound, 90% credible interval upper bound]: -0.52 [-0.67, -0.37]; log-odds of sleep efficiency hierarchical Bayesian regression (Gaussian): -0.20 [-0.35, -0.04]; sleep fragmentation hierarchical Bayesian regression (Gaussian): 0.20 [0.05, 0.35]). Baboons from different groups also showed greater temporal coordination in their sleep patterns during the night when they shared a sleep site compared to when they were sleeping in separate sites (temporal coordination score hierarchical Bayesian regression (Gaussian): 0.18 [0.00, 0.37]).

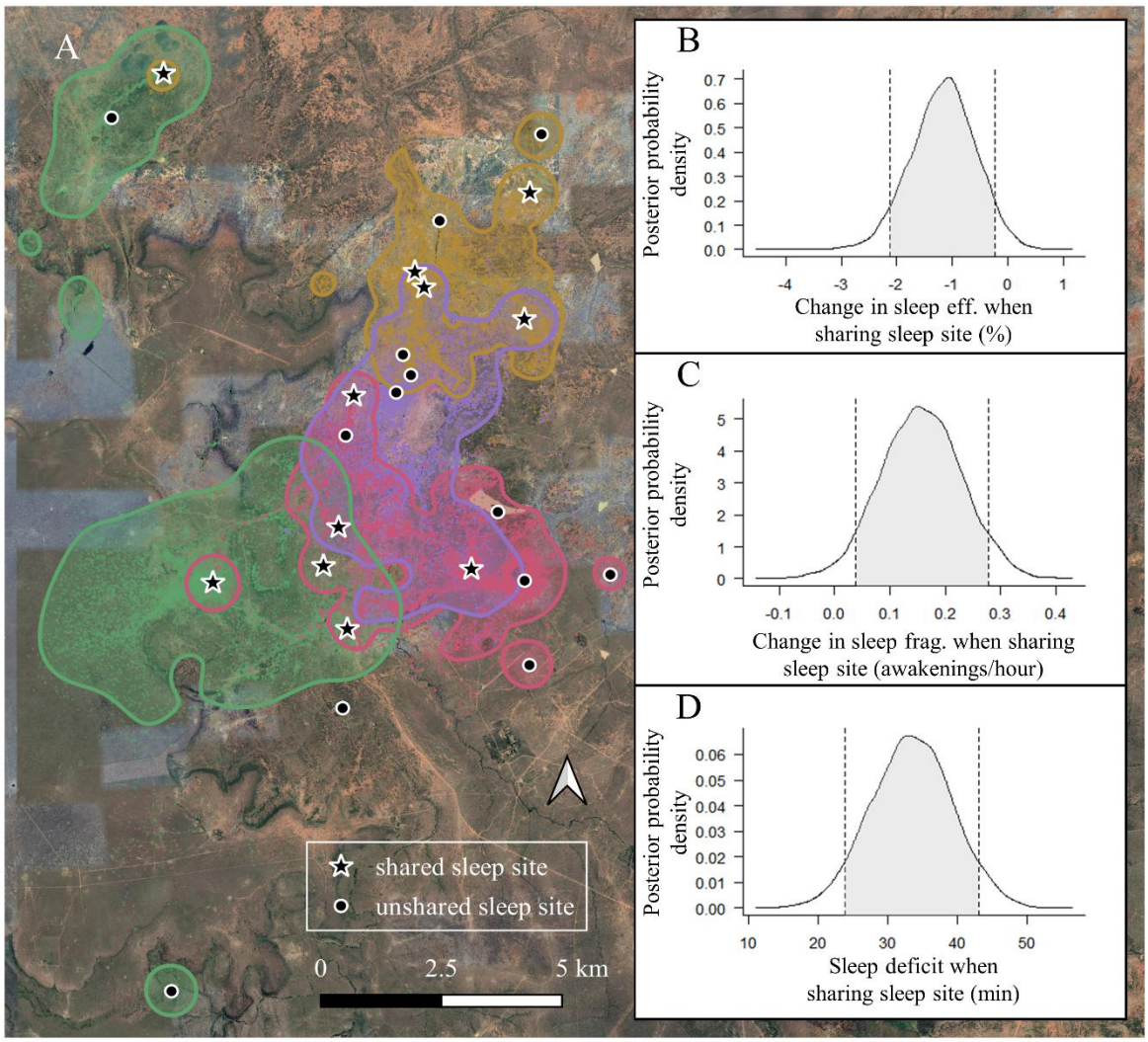

Figure 3.1. Social dynamics within shared sleep refuges disrupt the sleep of wild baboons. Baboon groups took refuge in trees and on cliffs during the night to mitigate the risk of predation while they fulfilled their physiological need for sleep. Scarcity of high-quality nighttime refuges led to overlap in the sleep site alternatives of neighboring groups (A). Although groups tolerated the simultaneous use of shared sleep sites, the altered social environment impaired sleep quality. When sleeping with another group, baboons experienced 1.2% less efficient sleep (B) and 0.15 more waking events per hour of sleep (C) during the sleep period, leading to a total of 33.5 minutes of sleep lost (D), on average, while at the sleep site. The home ranges of the four groups, determined by the 95% utilization distribution, as well as all GPS locations collected during the study are depicted in subplot A. Subplots B, C, and D show the posterior probability density of the effect size of sleeping with another group on the respective sleep metrics, with the 90% credible interval shaded and bound by vertical dotted lines.

Visualization of the groups' trajectories during the 123 inter-group encounters across the study period highlighted the central role that sharing a sleep site played in catalyzing and shaping these encounters. Baboon groups were 8.0 times more likely to have an interaction with a neighboring group on days following sharing a refuge with that particular neighbor compared to days prior to which groups slept at different sites (Fig. 3.2B; hierarchical Bayesian regression (Bernoulli): 2.84 [2.25, 3.47]). Spending the night together influenced not only the probability of an encounter the following day, but also the nature of the interaction that occurred during the encounter: when baboon groups did encounter each other, their interactions were 3.2 times more likely to involve extended, cohesive movements—similar to the coordinated movements of group-mates—if the participating groups spent the night at the same sleep site the previous night than if they had slept at separate sleep sites (Fig. 3.2C; 1.60 [0.82, 2.41]).

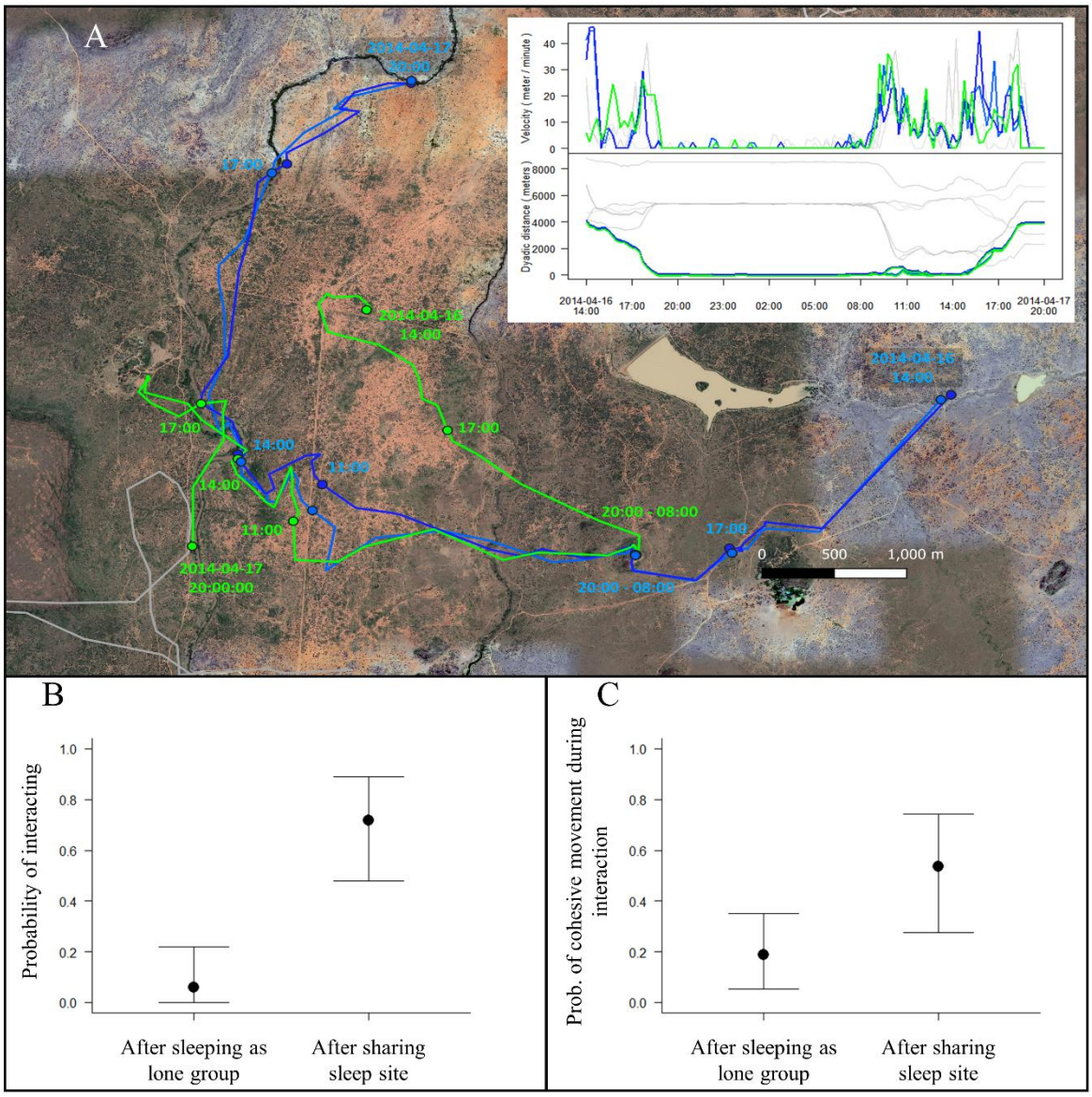

Figure 3.2. Shared sleep sites catalyze extended, cohesive movements between neighboring baboon groups. The social dynamics within the nighttime refuge continued beyond the sleep period, as baboons were substantially more likely to engage in an interaction with a neighboring group on days following a night spent in the same sleep site as that particular neighbor (B). Not only did sleeping in the same refuge play a central role in catalyzing interactions the following day, but it also shaped the nature of these interactions. When groups encountered each other, they were much more likely to engage in extended, tolerant interactions consisting of cohesive movements if they had spent the previous night together than if they had spent the previous night in different sleep sites (C). Subplot A shows the trajectories of study groups during a 30-hour period that illustrates an example of cohesive movement between neighboring groups. The green line in subplot A indicates the trajectory of one adult female, the two blue lines indicate the trajectories of two adult female group-mates, and grey lines indicate the trajectories of other study individuals not highlighted in this example. Line colors in the

inset correspond to the trajectories. Subplots B and C show the mean of the posterior linear predictions of the data from a model of the data, with error bars indicating the 90% credible interval.

The cohesive movements that occurred after groups slept in the same sleep site defined overall relationships of tolerance between groups across the study period, characterized by non-random inter-group attractions. When engaged in an encounter, groups maintained closer proximity to each other and had more similar trajectories—as indicated by similarities in their movement headings and velocities, as well as the dynamic time warping distance between the trajectories— than expected based on time-shifted movement trajectories (Fig. 3.3A, B; Fisher's exact tests: mean dyadic distance during encounters: $p < 0.0001$, difference in headings during encounters: $p < 0.0001$, difference in movement velocity during encounters: $p < 0.0001$, dynamic time warping distance between trajectories during encounters: $p < 0.002$). This influence on each other's movement during encounters created non-trivial patterns of attraction between groups, with study groups maintaining a significantly lower mean distance to each other and greater proportion of time engaged in encounters across the entire study period than expected by chance (Fig. 3.3C, D; Fisher's exact tests: mean dyadic distance: $p < 0.02$, proportion of time engaged in encounters: $p < 0.0001$). Overall patterns of attraction across the study period arose specifically from attractions between groups after they spent the previous night in the same sleep site: while the mean dyadic distance between groups was significantly lower than expected by chance on the day after groups shared a sleep site, the mean dyadic distance between groups that had not spent the previous night together did not deviate from expectation (Fig. S3.1; Fisher' exact tests: mean dyadic distance after sleeping in same sleep site: $p < 0.0001$, mean dyadic distance after sleeping in different sleep sites: $p = 0.253$). The outsized influence of interactions at the sleep site on overall relationships between groups is perhaps unsurprising, given that almost half (60/123) of all encounters occurred, at least partially, at the sleep site.

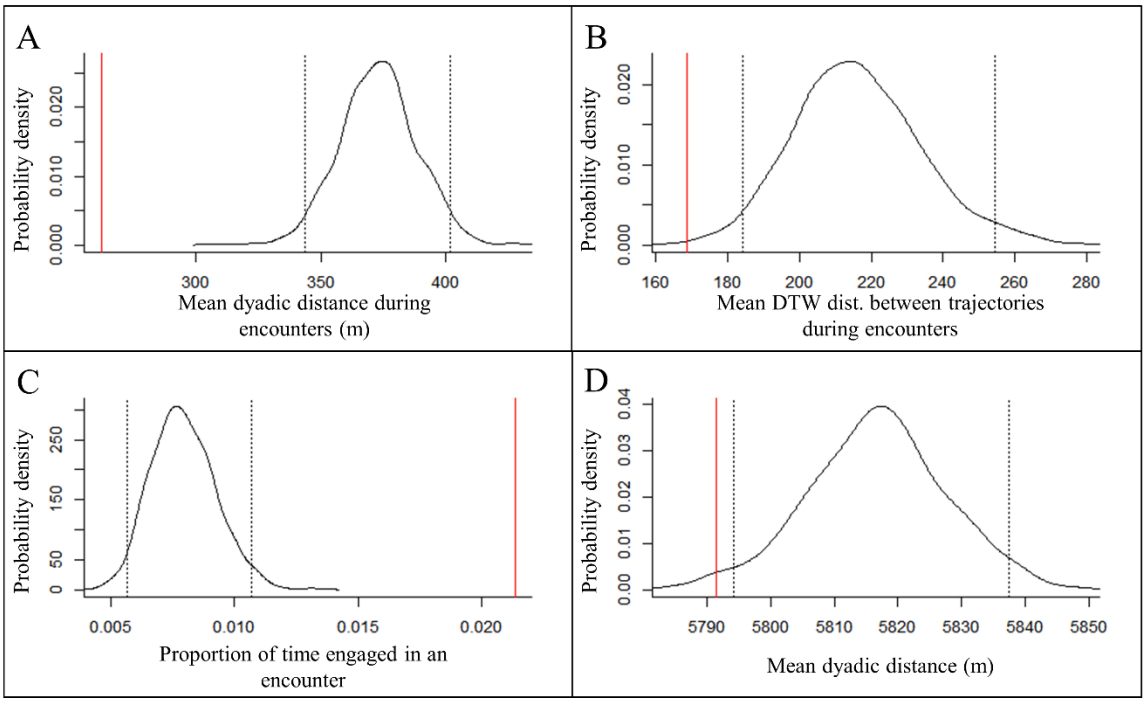

Figure 3.3. Overall relationships of tolerance between groups arise from the extended interactions that occur after sharing a sleep site. Across the study period, groups moved together more cohesively when they encountered each other than expected by chance, indicated by their proximity and the dynamic time warping distance between their movement paths when engaged in an encounter (A, B; Fisher's exact tests: mean dyadic distance during encounters: $p < 0.0001$, dynamic time warping distance between trajectories during encounters: $p < 0.002$). These cohesive movements resulted in neighboring groups spending more time engaged in encounters and maintaining an overall lower mean dyadic distance across the study period than expected by chance (C, D; Fisher's exact tests: proportion of time engaged in an encounter: $p < 0.0001$, mean dyadic distance: $p < 0.02$). In all subplots, the vertical red line represents the empirical value, while the black solid line represents the null distribution of the measure calculated from 1000 time-shifted datasets. The vertical black dotted lines delineate the 2.5 and 97.5 percentiles of the null distributions.

In contrast to their daytime movements, baboon groups exhibited no interdependence in their choice of sleep site. The empirical proportion of nights on which study groups slept with another group fell well within the null distribution that was generated from permutations of groups' sleep site occupancy time-series (Fig. S3.2; Fisher's exact test: $p = 0.291$). Thus, co-occurrence at the sleep site occurred randomly, with groups neither attracting nor avoiding each other at the sleep site.

Discussion

In this study, we demonstrate that the social dynamics surrounding sleep not only fundamentally influence sleep patterns, but also extend well beyond the sleep period, shaping the diurnal interactions, and even the broader relationships, between social animal groups. Coincidental congregation of neighboring baboon groups at shared sleep refuges results in social disruptions to sleep that are temporally coordinated across cohabitating groups. Although these social dynamics of sleep impair sleep quality, they play a central role in catalyzing tolerant inter-group encounters that extend beyond the sleep refuge and define the nature of relationships between groups in a species that is not known for particularly positive inter-group relations (Cheney & Seyfarth, 1977). These results highlight the importance of the physiological need for sleep, in conjunction with local ecological features (e.g. the abundance and distribution of sleep refuges), in shaping the social organization of a population, while also emphasizing the trade-offs that animals face when sleeping in a social context.

By measuring sleep via accelerometry, we shed much needed light on the influence of the social environment on sleep in the wild. Research on sleep has traditionally focused on isolated individuals in the laboratory, divorced from the ecologically and socially relevant context in which it evolved (Rattenborg et al., 2017; Reinhardt, 2020; Samson, 2021), and our understanding of how sleep manifests in the social environment in which it is embedded for many wild animals is therefore severely limited. Accelerometer-based sleep classification opens a new frontier of scientific investigation into the social dynamics of sleep in the wild, by dramatically increasing the ease of measuring sleep over relatively long durations and across several individuals simultaneously (Watanabe & Rutz, 2022). We took advantage of this opportunity to understand how sharing the nighttime refuge with a neighboring social group influences the sleep of wild baboons, revealing that baboons experience shorter duration, lower efficiency, and more fragmented sleep when spending the night with another group. This reduction in sleep quality may reflect an incidental sleep cost of chance encounters at the sleep site, perhaps resulting from the stress induced by inter-group interactions (Sanford et al., 2015; Wittig et al., 2016) or from a shortage of high-quality sleep positions within the sleep site that could accommodate the greater number of individuals (Smeltzer et al., 2022). However, we propose an alternative explanation: the decrease in sleep quality while sharing a sleep site may

represent adaptive sleep loss, whereby a sacrifice of sleep to engage in other activities results in net fitness benefits (Lesku et al., 2012). Recent studies of the collective dynamics of sleep within social groups also reveal social disruptions of sleep (Karamihalev et al., 2019; Loftus et al., 2022), and propose that the interactions that occur between individuals during coordinated periods of nocturnal wakefulness may prove beneficial to fitness (Loftus et al., 2022). The temporal coordination in nighttime waking patterns between the members of co-sleeping groups suggests that, surprisingly, these nighttime interactions may also arise across social group boundaries, raising the possibility that social sleep dynamics serve important functions in developing relations between, as well as within, groups.

Our results demonstrate that the social dynamics of sleep continue well beyond the sleep period, revealing bi-directional feedback between the social environment and sleep. High-quality sleep refuges are a critical, yet limited resource for many animals (Anderson, 1984; Markham et al., 2013), and these important resources could become hotspots of interaction simply by bringing conspecifics together in time and space. However, we found that sleeping together not only increased the likelihood of groups encountering each other the following day, but it also changed the very nature of their interactions: inter-group encounters were substantially more likely to involve extended, tolerant interactions after groups had slept together the previous night. Cooperative social interactions between members of distinct social groups may arise during the sleep period from both decreased foraging competition and the mutual benefit of increased collective vigilance and predator dilution (Lucchesi et al., 2020; Robinson & Barker, 2017), leading to the development of inter-group social bonds that then persist into the day (Leu et al., 2011). Although this study is the first, to our knowledge, to implicate social sleep dynamics as a formative influence on the relationships between non-human animal groups, a large body of evidence from research on humans suggests that interactions within the sleep period are indeed important in the development and maintenance of social bonds (reviewed in Gordon et al., 2017, 2021; Troxel, 2010; Troxel et al., 2007).

The interplay between the sleep and the social environment highlights the role that the physiological need for sleep may play as a key driver of complex forms of sociality. The evolution of multi-level societies, in which distinct social units occasionally exhibit highly coordinated behavior

within regular bouts of close proximity (Grueter et al., 2017), critically depends on tolerant relationships among social units (Grueter et al., 2012; Rubenstein & Hack, 2004). Here, we demonstrate that the search for a safe refuge in which to fulfill a sleep requirement catalyzed tolerant relationships between baboon groups, as mutual attraction to a limited number of sleep refuges brought about inter-group interactions—interactions that made up almost half of all encounters between groups (60/123) and that were largely tolerant due to the inter-group dynamics that occurred while sleeping within a shared refuge. Because these interactions arose from chance encounters at the sleep site, the tolerant inter-group relationships that represent the building blocks of multi-level societies may emerge spontaneously from a scarcity of adequate refuges in which to obtain high-quality sleep. Indeed, limitation of sleep refuges promotes conspecific interaction within diverse taxa (Childress & Herrnkind, 1997; Gardner et al., 2007), and may be important in shaping the social organization of a species (Duffield & Bull, 2002; Hamilton III, 1982; Martin & Martin, 2007). We note that many species that exhibit multi-level social organizations live in habitats in which refuges are scarce, and interactions between distinct social units often occur primarily at the sleep site (geladas: Bergman, 2010; hamadryas baboons: Kummer, 1968; Stammbach, 2008; vulterine guineafowl: Papageorgiou et al., 2019; reviewed in: Sueur et al., 2011; Grueter et al., 2012; Hamilton & Watt, 1970). Moreover, recent evidence that large brains are not a prerequisite for the evolution of multi-level societies lends support to a self-organized origin of this complex form of sociality (Papageorgiou et al., 2019).

Our findings offer a new perspective on the evolution of our own societies. Our earliest ancestors evolved in a rapidly expanding savannah that was dominated by diverse and abundant carnivore megafauna (Brain, 1970, 1983; Treves & Palmqvist, 2007; Werdelin & Lewis, 2005). Evidence suggests that early hominins faced intense predation pressure (Brain, 1983; Treves & Palmqvist, 2007), and thus they likely obtained their necessary sleep in safe refuges above the ground (Coolidge & Wynn, 2018; Samson & Nunn, 2015). Because these refuges would have been particularly sparse in the new savannah habitat, distinct hominin foraging groups may have aggregated at night, forming the first multi-family aggregations in our lineage (Aureli et al., 2008; reviewed in Grueter et al., 2012). As the formation of social groupings beyond the family unit

signified an integral step in the evolution of extensive cooperative networks in humans (Hill et al., 2011), we suggest that the intense cooperation and cumulative culture that make us so uniquely human may be partially attributable to the social dynamics of sleep in an environment with scarce refuges.

Materials and Methods

Data collection

We monitored the movement and activity patterns of six adult female olive baboons distributed across four stable social groups that range on Mpala Research Centre, a 200 km^2 conservancy of savannah-woodland habitat located on the Laikipia Plateau in central Kenya. Each study individual was trapped, anesthetized, and fit with a GPS and accelerometer collar (see Isbell et al. 2018 for details on capture methodology). We programmed the collars to record the baboon's GPS location at 15-minute sampling intervals and collect 3-second bursts of tri-axial accelerations for 3 s/min at 10.54 Hz/axis continuously throughout the study. The collars collected data from as early as January 15, 2014 to as late as January 27, 2015, with some collars ending data collection prematurely (Table S3.1). In total, we collected 1644 baboon-days of GPS data and 1646 baboon-nights of accelerometry data. We processed the data to synchronize the GPS location data across groups, interpolate missing fixes, correct anomalous GPS fixes, and remove local GPS jitter that was likely caused by error (see Supplemental Materials).

Identifying home ranges and sleep sites

We created group-level tracks based on the tracks of collared females. The average dyadic distance of females belonging to the same group was 43.4 ± 0.3 m (mean ± SE), falling within the typical range of baboon group spread (Harel et al., 2021), and thus, data from a single group member was sufficient to describe the location of the group. We therefore removed group-level duplicate data (i.e. data on two females belonging to the same group) when sampled simultaneously. We then determine the utilization distribution (UD) for each group using kernel density estimation (KDE). We define each group's home range as the minimum boundary encompassing 95% of the UD. For each group dyad, we calculated the proportion of overlap of the groups' home ranges, as well as the Bhattacharyya's affinity between their UDs for a more accurate probability of the groups' joint space

use (Fieberg & Kochanny, 2005; Table S3.2, S3.3). For all home range analyses, we used the "adehabitatHR" package (Calenge, 2006) for R version 4.1.2 (R Core Team, 2021).

We determined where each individual spent each night by calculating the mean location of her GPS fixes from 20:00 to 04:00. With hierarchical agglomerative clustering of these mean nighttime locations, we identified 24 distinct sleep sites used by the study population. We used the cluster membership of individuals' mean nighttime locations to determine in which sleep site they took refuge each night.

Sleep analysis

We extracted sleep metrics from the accelerometry data with an adaptation of the algorithms presented by van Hees and colleagues (2015, 2018) that were developed for analyzing sleep in humans from wearable accelerometry devices. Our adaptation of the sleep classification algorithm, which was implemented and validated in Loftus et al. (2022), exhibited 80.7% accuracy in distinguishing sleep and waking behavior in wild olive baboons. Using the accelerometer-based sleep classification algorithm, we calculated 1) the total time spent sleeping at the sleep site, 2) sleep efficiency during the sleep period, and 3) sleep fragmentation during the sleep period. We also measured the temporal coordination score in sleep and wake patterns for each dyad of individuals on each night (see Supplemental Materials for details of sleep classification algorithm and definitions of sleep metrics).

Encounter analysis

We created animations of inter-group encounters to observe and analyze interactions that occurred during encounters. We calculated the Euclidean distance between every dyad of study groups at each timestamp and defined dyadic inter-group encounters as periods when any member of a group was within the response distance (i.e. the distance at which groups typically react to the presence of another group) of a member of another group. We developed an algorithm to extract this response distance empirically from the data, and determined it to be 600 m (Fig. S3.3, see Supplemental Materials for further details). For each dyadic encounter, we recorded all instances of: 1) moving cohesively, 2) co-sleeping, 3) following/pursuing, 4) avoiding, 5) displacing, 6) avoiding at a sleep site, 7) displacing from a sleep site, and 8) moving indifferently to one another. Although

group encounters were extracted using data from all study individuals and the locations of all collared individuals were visualized in the animations, interactions were only scored at the group dyad level, as collared group-mates exhibited the same general behaviors during encounters.

For this analysis, we defined the sleep site as the location in the animation where the group took refuge for the duration of the night, and we considered any encounter that involved sharing a sleep site, avoidance at a sleep site, or displacement from a sleep site to have occurred at least partially at a sleep site. We note that we defined encounters between groups purely based on spatial proximity, whereas we defined inter-group interactions by the manual scoring of the animations of the encounters (described above). Thus, two groups could share a sleep site without interacting the following morning if they departed from the sleep site with apparent indifference to one another, even though they were considered to be engaged in an encounter during their morning departure (based on spatial proximity).

Intergroup movement and sleep site occupancy analysis

We analyzed how the interdependencies in the movements and sleep site choices of groups across the entire study period compared to that expected by random chance to understand the nature of the broader relationships between the groups. We first explored whether groups avoided each other or were generally attracted to each other, by measuring the mean dyadic distance between each group dyad, as well as the proportion of time that dyads spent in an encounter. We again considered an encounter to occur when individuals from different groups were within the response distance of 600 m (Fig. S3.3). We compared these values to those calculated from 1000 permutations of the groups' movement paths (see Supplemental Materials for details). To understand how behavior during encounters compared to that expected by chance, we calculated the following measures in the empirical data, limited to the time when two groups were within the response distance of each other: 1) the mean distance between the two groups, 2) the mean difference between the headings of the groups, 3) the mean difference between the step lengths (e.g. displacements between each 15-minute interval) of the groups, and 4) the mean distance between the groups movement trajectory time-series, as determined by dynamic time warping (Bellman & Kalaba, 1959). We again compared these measures to those calculated from the movement path permutations. We then repeated this movement

path permutation analysis, comparing the mean dyadic distance between groups in the empirical and permuted datasets, but after separating both the empirical and permuted datasets into data from days on which groups had slept at the same sleep site the prior night and data from days on which groups had slept in separate sleep sites the prior night.

We assessed whether groups influenced each other's sleep site choices, by determining whether groups shared a nighttime refuge more or less than expected by chance. Specifically, we compared the proportion of nights during which two groups slept at the same sleep site to 1000 such proportions, each produced by applying a random shift to one dyad member's sleep site occupancy time-series (see Supplemental Materials for details).

Statistical analysis

We tested the influence of spending the night at a sleep site with another group on the total sleep time, sleep efficiency, and sleep fragmentation. We modelled the total sleep time while at the sleep site using a hierarchical Bayesian regression model of family Student-t, with a fixed effect variable indicating whether the group was sharing its sleep site on that night with another group, and random intercept terms for group identity, individual identity, date, and the identity of the sleep site. By including the identity of the sleep site as a random effect, we controlled for variation among the sleep sites in their characteristics that may inherently promote or hinder high-quality sleep. We used the same fixed and random effect variables to model the log odds of the sleep efficiency, as well as sleep fragmentation, both with hierarchical Bayesian regression. We then tested whether individuals from different groups were more likely to show temporal coordination in their nighttime sleep-wake patterns when they spent the night in the same sleep site. We modelled the temporal coordination score between each dyad as a function of whether dyad members were spending the night in the same sleep site, using hierarchical Bayesian regression. We included random intercepts for the identity of both dyad members, as well as for the identity of the dyad itself. We removed data from dyads of individuals that belonged to the same group prior to analysis.

To test how sharing a sleep site influenced inter-group interactions the following day, we modelled the probability of two groups engaging in an interaction as a function of whether the two groups had spent the night in the same sleep site the previous night with hierarchical Bayesian

regression of family Bernoulli. We included random intercept terms for the identity of both groups, individually, as well as for the identity of the group dyad. We then subset the data to instances in which two groups encountered each other and modelled the probability of the encounter involving cohesive movement (encounter outcome (1) in *Encounter analysis*) as a function of whether the two groups had slept in the same sleep site the previous night. We again used hierarchical Bayesian regression of family Bernoulli, with random intercept terms for the identity of each group involved in the encounter and the identity of the group dyad.

For all permutation tests, we compared empirical values to their respective null distributions with a Fisher's exact test. The p-value therefore represents the proportion of values from the null distribution that are as extreme or more extreme than the empirical value.

We fit all Bayesian models with the "brms" package in R (Bürkner, 2017). We used diffuse, mean-zero Gaussian priors for fixed effects variables. For random effects variables and the intercept, we used half Student-t distributions with three degrees of freedom and a scale parameter of 2.5 as prior distributions. Model estimates are based off of four independent Hamiltonian Monte Carlo chains with 2500 burn-in iterations and 2500 sampling iterations. Trace plots indicated adequate mixing and convergence of the four chains on the same posterior region. In the main text, we report the mean of the posterior distribution, along with the lower and upper 90% credible interval bounds from the standardized models for all model estimates. The model output tables and the posterior predictive checks are contained in the Supplemental Materials.

Data availability

GPS and accelerometry data generated during this study are stored in the Movebank data repository (www.movebank.org) under the project name "Leopards, vervets, and baboons in Laikipia, Kenya". For permission and access to download the data from Movebank, please contact Lynne Isbell (laisbell@ucdavis.edu). The data resulting from observations of animations of the GPS data during inter-group encounters are publicly available for download at Dryad (https://doi.org/10.25338/B87D15). All code and instructions necessary to reproduce the final results from the raw data are published on GitHub (https://github.com/CarterLoftus/intergroup_sleep/) and archived on Zenodo (https://doi.org/10.5281/zenodo.6912917).

Supplemental Materials

Materials and Methods

Data processing

We fit six adult female baboons across four social groups with GPS collars that contained a tri-axial accelerometer unit. We programmed each GPS collar to collect location data (henceforth, fixes) every 15 minutes. However, due to variation in the time the collars needed to acquire and record a fix, they did not collect fixes exactly according to the programmed sampling schedule or in perfect synchrony with each other. We required synchronous location data across the population to analyze the distance between neighboring groups, as well as their trajectories with respect to one another. We therefore interpolated fixes at the ideal sampling schedule (i.e. every 15 minutes, on the minute) with a linear interpolation, when at least one fix was taken within 7.5 minutes of the sampling timestamp.

Using this new dataset, with location data interpolated to the programmed sampling schedule, we further interpolated locations for missing and anomalous data. We performed a linear interpolation for timestamps on which the collars failed to collect a GPS location, under the condition that both the prior and subsequent fix were within 60 minutes of the timestamp of the location to be interpolated and within 75 minutes of each other. The location data for 3252 failed fixes (2.1% of all location data) were interpolated in this way. To assess the validity of this interpolation method, we used the same method to interpolate location data for timestamps associated with successful fixes. We found that interpolated locations showed a median distance of 15.6 m (mean: 38.1 m) away from the true fix taken at that timestamp. We considered GPS fixes anomalous if their distance to the associated interpolated location was greater than the 99^{th} percentile of the distances between GPS fixes and associated interpolated locations. We replaced these anomalous data with the interpolated locations, resulting in a total of 1504 anomalous locations (1.0% of all location data) that were replaced by their associated interpolated locations.

After interpolating missing and anomalous GPS fixes, we removed the local GPS movements from the data that were likely caused by minor GPS error (jitter) by applying a 30 m spatial discretization to the location data. For the spatial discretization, we considered the first location of

each individual to be its first spatially discretized location as well. We then iteratively measured the distance from each GPS location to the individual's previous spatially discretized location. If this distance was greater than 30 m, then the location of the baboon's current GPS fix was taken to be the individual's current spatially discretized location. If, however, the distance was not greater than 30 m, then the baboon's previous spatially discretized location was taken to be its current spatially discretized location. We used the individual's spatially discretized location in all analyses of locations and trajectories, aside from the identification of sleep location. For the identification of sleep location, averaging the location of multiple GPS fixes during the night (see *Home range analysis and sleep site identification* in the main text) eliminated concerns about GPS error. For all data processing and subsequent analyses, GPS data was reprojected from latitude-longitude to UTM coordinates.

We programmed the tri-axial accelerometer unit contained in each GPS collar to collect a three second burst of accelerometry data at 10.54 Hz per axis at the beginning of every minute. After data collection, we calculated the vectorial dynamic body acceleration (VeDBA), a commonly used measure of overall activity (Qasem et al., 2012), using a 0.7-second time window, and took the natural logarithm of the mean of the VeDBA (henceforth, log VeDBA) over each three-second burst.

One collared female died during data collection, and we removed data prior to her death before analysis to prevent anomalous behavior biasing our results. Specifically, we removed both GPS and accelerometry data collected by her collar after May 27, 2014, because on the following day, she became separated from her group, and remained apart from the group for much of the remainder of her life (i.e. until June 8, 2014), even during the sleep period (indicated by the GPS locations of her healthy group-mate). This behavior is highly unusual for female baboons, which maintain high cohesion with group-mates throughout their lives, and thus, we felt justified in removing data associated with this anomalous behavior.

Measuring sleep from accelerometry

We extracted metrics of sleep from accelerometry data with an algorithm that we had previously developed and validated for use in measuring sleep behavior in baboons (Loftus et al., 2022). In the validation study, the algorithm exhibited an accuracy of 80.7% in differentiating the sleep vs. waking behavior of wild baboons (Loftus et al., 2022). The algorithm, which is adapted from

a method of classifying sleep behavior and determining the sleep period in humans from wearable devices (van Hees et al., 2015, 2018), first identifies the sleep period, by connecting periods of sustained inactivity that occur within short succession of each other. For each noon-to-noon period, we took the rolling median of an individual's log VeDBA over a nine-minute window, and classified minutes as potential sleep epochs when the rolling median of the log VeDBA was less than the 10^{th} percentile of these values during this 24-hour period multiplied by 1.125. Continuous blocks of potential sleep epochs that were individually greater than 30 minutes in duration but less than 45 minutes apart from each other were then combined into potential sleep periods. The longest potential sleep period during the noon-to-noon period was then identified as the sleep period. Both within and outside of the algorithmically determined sleep period, we classified epochs as sleep behavior if they occurred within bouts of at least three consecutive epochs in which the log VeDBA remained below the 10^{th} percentile of the rolling median of the log VeDBA during the 24-hour period multiplied by 1.125. This procedure identified the sleep period for 1627 baboon-nights of data.

After classifying sleep behavior and identifying the sleep period, we calculated total time spent sleeping, sleep efficiency, and sleep fragmentation. Typically, total time spent sleeping would be calculated as the total number of epochs of sleep within the sleep period. However, individuals' extended periods of activity during the night truncated their sleep period dramatically on several nights of the study period, resulting in a heavily skewed distribution of the total number of epochs of sleep within the sleep period (Fig. S3.4). We therefore chose to measure total time spent sleeping as the total number of epochs of sleep between the median arrival time at the sleep site and the median departure time from the sleep site the following morning, as using standardized times across nights and individuals eliminated heavy skew in the distribution. An individual's sleep site arrival time was the first time after 12:00 on which it entered a 200 m radius of its mean nighttime (20:00 – 04:00) location, and an individual's sleep site departure time the following day was the first time that an individual left the same 200 m radius of the mean nighttime location. If an individual never left the 200 m radius of its previous nighttime location on a given day, then the departure time was set to 12:00 (5 departure times were assigned this way, of the 1617 departure times that were assigned).

Across all individuals and all nights, the median arrival time at the sleep site was 17:30, while the median departure time was 08:30.

We calculated sleep efficiency as the proportion of epochs during the sleep period that are classified as sleep, and sleep fragmentation as the number of distinct wake bouts during the sleep period that were greater than or equal to two minutes in duration, divided by the total number of hours of sleep during the sleep period, following (Samson & Nunn, 2015). These sleep metrics were not sensitive to skew in the sleep period duration or total number of epochs of sleep during the sleep period, and so we did not have to limit their calculation to standardized time periods.

We used the minute-by-minute classification of sleep behavior to evaluate temporal coordination in the periods of sleep and waking between study individuals while at the sleep site. On each night and for each dyad of individuals, we calculated a temporal coordination score as the number of minutes in which individuals exhibited the same behavior (either sleep or waking) divided by the total number of minutes in which we had accelerometry data (and thus, sleep behavior data) for both individuals. These calculations were limited to the period between the median time of arrival at the sleep site (17:30) and the median time of departure from the sleep site (08:30; medians calculated across all individuals for the study period).

Prior to analysis, we removed all sleep data (both minute-by-minute and nightly measures) on nights during which the accelerometer units frequently failed to collect data, as incomplete data may bias the threshold value used for sleep classification on these nights. Specifically, we removed data from noon-to-noon periods missing at least 120 (8.3%) accelerometry bursts. This data cleaning resulted in the removal of nine nights of data, leaving a total of 1618 baboon-nights of sleep data.

Determining the response distance

To understand how the social dynamics within the sleep site affected inter-group relations, we analyzed the influence that sharing a sleep site with a neighboring group had on the quantity and nature of interactions with that group the following day, as well as the broader encounters between study groups over the full study period. However, prior to these analyses, we had to define an inter-group encounter. As opposed to estimating, somewhat arbitrarily, a distance between groups at which we would consider them to have engaged in an encounter, we chose to define this distance directly

from the empirical data, as the distance at which groups respond to each other's presence. To determine the distance at which groups respond to each other's presence, we established candidate response distance intervals from 0 to 7000 m, with each distance interval spanning 100 m (i.e. [0, 100), [100, 200), [200, 300), ..., [6900, 7000)). For each distance interval, we extracted the total number of instances in the empirical data in which the distance between two groups (i.e. dyadic distance) fell within that distance interval (Fig. S3.3, red points). We then repeated this procedure 1000 times, but instead of extracting the number of instances within each distance interval from the empirical data, we extracted this metric from a new time-shifted dataset for each repetition. In each time-shifted dataset, each individual's time series of locations had been independently shifted by a random number of days, such that study animals maintained their true trajectories, but trajectories were shifted in time with respect to one another. These time-shifted datasets produced a null distribution for each distance interval of the total number of instances in which groups were separated by a distance within that interval (Fig. S3.3, semi-transparent black points) while controlling for mutual attraction to resources and maintaining the spatio-temporal autocorrelation inherent to the data (Havmøller et al., 2021).

We then compared the empirical values in each distance interval to the null distribution within the same distance interval to determine at which distances groups' co-occurrence deviated from that expected by chance. We considered the maximum distance at which baboon groups respond to each other, and thus, the encounter distance threshold for our analyses, to be the lower bound of the first distance interval, starting from 0, in which the empirical value fell between the 5^{th} and 95^{th} percentile (Fig. S3.3, blue bars). Using this method, we found the response distance to be 600 m.

When shifting the data in time, we took measures to ensure that the null distributions were unbiased. First, we applied all shifts within 30-day segments of data, so that no trajectories could be compared to the trajectories of other individuals that were more than 30 days apart, as ephemeral resources may become variable at this time scale. Secondly, we only extracted metrics that contributed to the empirical values and the null distributions from 30-day segments of an individual's data when the individual had a complete dataset for those 30 days (i.e. never an entire day, or more, of data missing within the segment).

We removed the data from Pa_LI_TH and Pa_AI_WG for this analysis, as these data were redundant with the data from their respective group-mates, who each had a longer duration of data collection than the individuals excluded. We also limited this analysis to the period between 09:00 and 17:00 (30 minutes after and before the median time at which groups depart from and arrive at their sleep sites, respectively), as data collected during the night did not inform how baboons responded to neighboring groups, seeing that groups were predominantly stationary while inhabiting their sleep site (Isbell et al., 2017).

Encounter analysis

We explored how groups responded when they encountered one another by analyzing animations of each inter-group encounter in Google Earth Pro v. 7.3.4.8248. To extract distinct inter-group encounters for visualization, we first calculated the Euclidean distance between every dyad of individuals at each 15-minute interval throughout the study. We defined dyadic inter-group encounters as periods when any member of a group was within the response distance (i.e. the distance at which groups typically react to the presence of another group) to a member of another group. We determined this response distance—identified as the maximum distance at which baboon groups' movements with respect to each other deviated from that expected by random chance—to be 600 m (Fig. S3.3, see *Determining the response distance* for further details). We extracted distinct encounters by combining any encounters that involved the same group dyad and that were separated by 60 minutes or less. For each distinct encounter, we recorded all instances of: 1) both groups moving cohesively together, similar to how two group-mates would move (cohesive movement), 2) both groups sleeping at the same sleep site (co-sleeping), 3) one group consistently orienting its motion towards the other group (following/pursuing), 4) one group consistently orienting its motion away from the other group (avoiding), 5) one group moving to the position where the other group is located, followed by the other group moving away (displacing), 6) one group re-orienting away from sleep site that the other group has inhabited (avoiding sleep site), 7) one group moving to the sleep site where the other group is located, followed by the other group leaving the sleep site (displacing from sleep site), and 8) the groups apparently moving with complete indifference to one another. Although group encounters were extracted using data from all study individuals, and the locations of

all collared individuals were visualized in the animations, encounters were only scored at the group dyad level, as collared group-mates exhibited the same general behaviors during encounters.

For this analysis, we defined the sleep site as the location in the animation where the group took refuge for the duration of the night, and any encounter that involved sharing a sleep site, avoidance at a sleep site, or displacement from a sleep site was considered to occur at least partially at a sleep site.

Movement path and sleep site permutations

We performed a movement path permutation procedure to assess how the relationships between the locations and trajectories of neighboring groups compared to that expected by random chance. We first measured the mean dyadic distance across all group dyads for the study duration, as well as the proportion of all dyadic distances calculated between all groups that were within the response distance (600 m; see *Determining response distance*). We then subset the data to only those instances in which a group dyad was engaged in an encounter (i.e. within the response threshold) and calculated, for the groups engaged in the encounter, 1) the mean distance between the groups, 2) the mean difference between the movement headings of the groups, 3) the mean difference between the step lengths (movement velocities) of the groups, and 4) the mean distance between the groups' movement trajectories, as determined by dynamic time warping (the total dynamic time warping distance, divided by the number of fixes in the movement trajectories; Bellman & Kalaba, 1959). We compared each of these measures, calculated from the empirical data, to 1000 respective measures, each calculated from a different permutation of the movement trajectories over the study period.

We used a similar time-shifting procedure as that described above (see *Determining the response distance*), in which we applied a random time-shift of a multiple of 15 minutes (the GPS sampling rate) to each individual's trajectory to produce datasets of permuted movement trajectories. As in the determination of the response distance, we applied time shifts to 30-day segments of data, and only extracted empirical and permuted metrics from 30-day segments of individuals' data that contained no full days of missing GPS data. Because this analysis was also performed at the group-level, we removed data from Pa_LI_TH and Pa_AI_WG prior to the calculation of metrics of interest in the empirical and permuted datasets. We again limited data for this analysis to the period between

09:00 and 17:00, to understand how groups influence each other's movements during the day, independent of how they may influence each other's choice of sleep site.

After finding that groups showed non-random attractions to each other over the full study period (Fig. 3.3, main text), we aimed to isolate whether these patterns resulted from attractions across the full study period or whether they resulted specifically from attractions that occur on the day after two groups spent the night at the same sleep site. We therefore repeated the time-shifting procedure with the same restrictions, shifting each individual's trajectory by a random number of days (again, within 30-day segments) for each of 1000 permuted datasets. For the empirical dataset and each permuted dataset, we separated the data into days on which group dyads had slept at the same sleep site the prior night and days on which group dyads slept at separate sleep sites the prior night. We then compared the mean dyadic distance following nights of group co-sleeping in the empirical data to that in the permuted data, and the mean dyadic distance following nights without group co-sleeping in the empirical data to that in the permuted data.

To understand whether groups influence each other's sleep site choices, we again compared empirical data to a null distribution produced from a permutation of the data. We determined where each group slept on each night (see *Home range analysis and sleep site identification* in main text) and measured the proportion of all dyad-nights in which two groups slept at the same sleep site. We compared this empirical proportion to a null distribution generated by calculating the same proportion from each of 1000 permuted datasets. We produced each permuted dataset by applying a random shift to the time-series of each group's sleep occupancy. As in the permutation procedures described above, we applied shifts to 30-day segments of data. Although we did not expect the sleep sites themselves to change markedly over larger time periods, the location of food resources, which are more likely to vary beyond this time scale, can influence the choice of sleep site (Chapman et al., 1989).

We used a permutation approach to analyze inter-group relationships, because apparent interdependencies in the movement and space use decisions of neighboring groups can potentially arise by chance. These spurious correlations between the movements of neighboring groups can result from shared, yet unmeasured environmental features, such as the location of food resources or barriers in the landscape, driving the movement choices of each group independently, while producing similar

decision outcomes (Spiegel et al., 2016). The permutation procedure allowed us to create a null distribution that controlled for the influence of the shared physical environment on the movements of neighboring groups.

Tables and Figures

Individual ID	Group ID	Start date of data collection	End date of data collection
Pa_AI_WG	AI	2014-01-19	2014-10-10
Pa_AI_YK	AI	2014-01-19	2015-01-15
Pa_LI_LU	LI	2014-01-15	2014-06-29
Pa_LI_TH	LI	2014-01-15	2014-06-08*
Pa_MG_SH	MG	2014-01-23	2015-01-08
Pa_ST_MS	ST	2014-01-16	2015-01-27

Table S3.1. Individual metadata. The table contains the identity of each baboon that was captured and collared with a GPS/accelerometry tag as part of this study, in addition to the group to which each individual belonged, and the start and end date of data collection from their collars (both accelerometry and GPS). The asterisk denotes that although Pa_LI_TH's collar continued to collect data until her death on 2014-06-08, we removed data collected by her collar after 2014-05-27 from the analysis, because after this date, her behavior became highly anomalous, likely as a result of her worsening condition that led to her death. She most likely became too ill to climb into a tree to sleep, and was eventually killed by a GPS-collared leopard on a small kopje during the night (Isbell et al., 2018).

	AI	LI	MG	ST
AI	-	0.063	0.007	0.156
LI	0.114	-	0.255	0.526
MG	0.018	0.369	-	0.002
ST	0.294	0.551	0.001	-

Table S3.2. Proportion of home range overlap between the study groups. If the row index is represented by i, and the column index is represented by j, then the proportion of home range overlap between animals i and j is equal to the area of intersection of the two home ranges divided by the area of animal i's home range.

	AI	LI	MG	ST
AI	-	0.062	0.015	0.245
LI	-	-	0.350	0.588
MG	-		-	0.072
ST	-	-	-	-

Table S3.3. Bhattacharyya's affinity between the home ranges of the study groups. Bhattacharyya's affinity is essentially a measure of the joint probability distribution of both animals' utilization distribution (UD), thus giving the probability of both animals occupying the area of home range overlap (Fieberg & Kochanny, 2005).

Bhattacharyya's affinity is calculated as $\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\sqrt{UD_i(x,y)} \times \sqrt{UD_j(x,y)}\,dxdy$, where UD_i and UD_j are the utilization distributions for animals i and j, respectively, and x and y are spatial coordinates. We note that although some group dyads have low overlap in their utilization distributions, as indicated by Bhattacharyya's affinity, all dyads have non-zero Bhattacharyya's affinities, and thus, could potentially encounter each other based strictly upon the spatial arrangements of their home ranges. We therefore included all group dyads in the analyses.

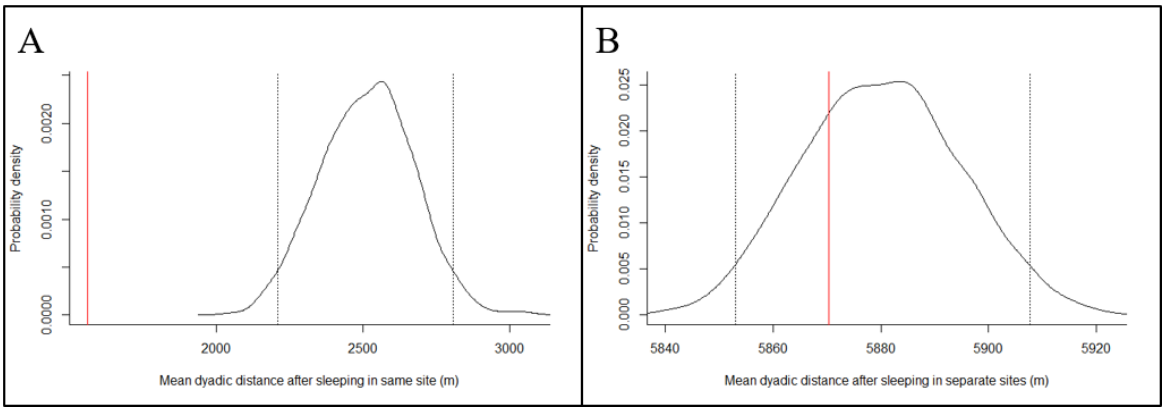

Figure S3.1. Results from the movement trajectory permutation procedure in which data from days following nights of sleeping with another group and data from days following nights sleeping as a lone group were analyzed separately. Comparison of the empirical mean dyadic distances between groups (vertical red lines) to the 2.5 and 97.5 percentiles (vertical black dotted lines) of the corresponding null distributions (black distribution lines) reveals that groups showed significantly lower dyadic distances than expected by chance after they slept at the same site (A; Fisher's exact test: $p < 0.0001$), but not after sleeping at separate sites (B; Fisher's exact test: $p = 0.253$). These results suggest that the overall non-random attractions between groups during the study period (Fig. 3.3, main text) can be directly attributed to deviations from expected behavior after two groups spent the night at the same sleep site.

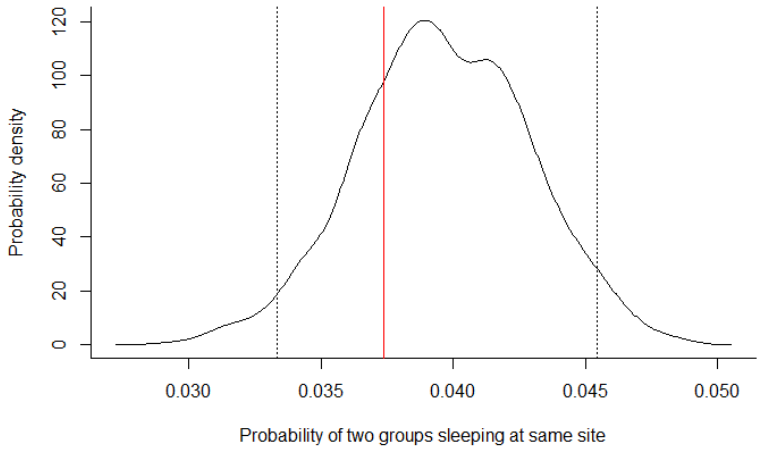

Figure S3.2. Results from the sleep site permutation procedure. Comparison of the empirical probability of two groups sleeping at the same sleep site (vertical red line) to the 2.5 and 97.5 percentiles (vertical black dotted lines) of the corresponding null distribution (black distribution line) shows that groups slept at the same sleep site with a frequency expected by chance (Fisher's exact test: $p = 0.291$), indicating that baboon groups did not avoid or prefer sleep sites that were occupied by neighboring groups when choosing where to settle down for the night.

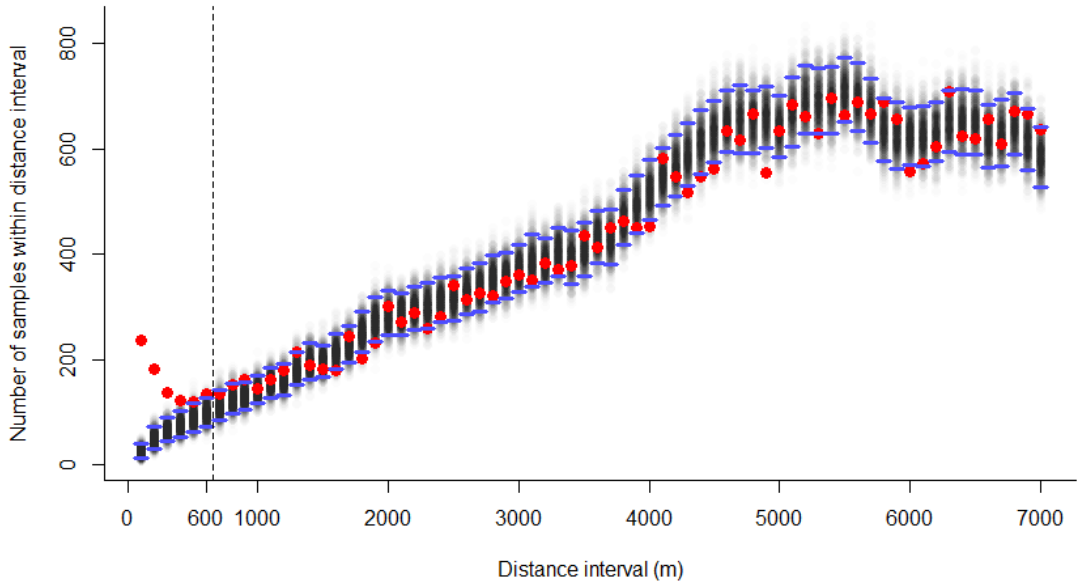

Figure S3.3. Results of the response distance analysis, indicating that baboon groups respond to each other's presence at distances of up to 600 meters. At each 100-meter interval, the number of instances in which the dyadic distance between study groups fell within this distance interval is plotted with a semi-transparent black

point for each of 1000 permutations of the movement trajectories. The 5th and 95th percentile of the null distribution at each distance interval is marked with a blue bar. The empirical number of instances in which the dyadic distance between study groups fell into each distance interval is marked with red points. Points are plotted at the upper bound of the distance interval to which they correspond (i.e. points plotted at distance interval 100 correspond to the distance interval [0, 100)). Because the [600, 700) distance interval is the first interval (when ascending from zero) in which the empirical value falls within the 5th and 95th percentile of the corresponding null distribution, we determined that baboon groups detect and respond to neighboring groups at up to 600 meters, indicated here with a black dashed line.

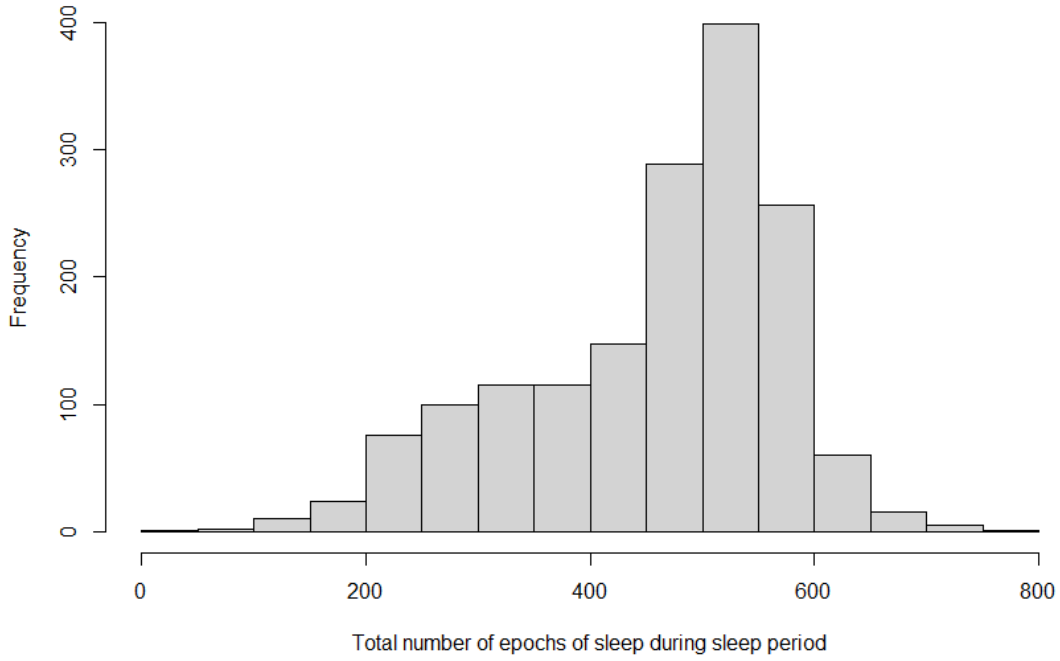

Figure S3.4. Histogram of the total number of sleep epochs during the sleep period, with the sleep period identified using a modification of the algorithm presented in (van Hees et al., 2018). Because of the large skew in the distribution of this measure, we chose to instead measure total sleep time as the total number of sleep epochs between the median time that individuals arrived at their sleep site (17:30) and the median time that individuals departed from their sleep site the following day (08:30).

Model output tables and posterior predictive checks

	Total sleep time at the sleep site (standardized)	
Predictors	*Estimates*	*CI (90%)*
Intercept	-0.11	-1.06 – 0.87

Group dyad sleeping at same site	-0.52	-0.67 – -0.37
Random Effects		
σ^2	0.66	
$\tau_{00\ group}$	0.83	
$\tau_{00\ group:tag}$	0.48	
$\tau_{00\ night}$	0.03	
$\tau_{00\ sleep\_clus}$	0.35	
ICC	0.72	
N_{sleep_clus}	24	
N_{group}	4	
N_{tag}	6	
N_{night}	377	
Observations	1611	
Marginal R^2 / Conditional R^2	0.019 / 0.372	

Table S3.4. Model output table of the model of total sleep time between the median sleep site arrival time and median sleep site departure time. The response variable (total sleep time) is standardized.

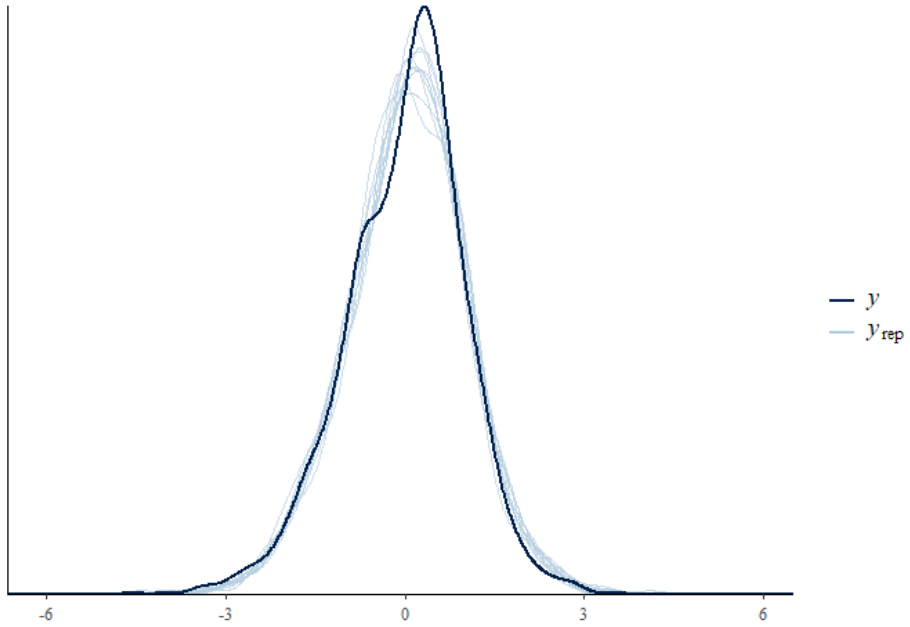

Figure S3.5. Posterior predictive check of the model of total sleep time between the median sleep site arrival time and median sleep site departure time. The response variable (total sleep time) is standardized.

	Log-odds of sleep efficiency (standardized)	
Predictors	*Estimates*	*CI (90%)*
Intercept	0.05	-0.75 – 0.75
Group dyad sleeping at same site	-0.20	-0.35 – -0.04
Random Effects		
σ^2	0.77	
$\tau_{00\ group}$	0.44	
$\tau_{00\ group:tag}$	0.34	
$\tau_{00\ night}$	0.03	

$\tau_{00\ sleep\_clus}$	0.06
ICC	0.53
N_{sleep_clus}	24
N_{group}	4
N_{tag}	6
N_{night}	377
Observations	1611
Marginal R^2 / Conditional R^2	0.003 / 0.236

Table S3.5. Model output table of the model of the log-odds of the sleep efficiency during the sleep period. The response variable (log-odds of the sleep efficiency) is standardized.

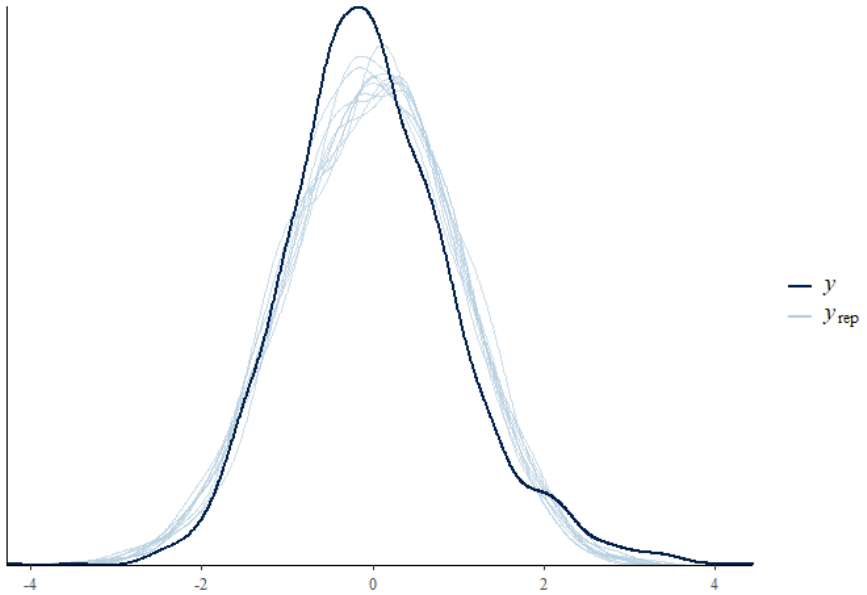

Figure S3.6. Posterior predictive check of the model of the log-odds of the sleep efficiency during the sleep period. The response variable (log-odds of the sleep efficiency) is standardized.

	Sleep fragmentation (standardized)	
Predictors	*Estimates*	*CI (90%)*
Intercept	0.06	-0.73 – 0.83
Group dyad sleeping at same site	0.20	0.05 – 0.35
Random Effects		
σ^2	0.77	
$\tau_{00\ group}$	0.55	
$\tau_{00\ group:tag}$	0.22	
$\tau_{00\ night}$	0.01	
$\tau_{00\ sleep\_clus}$	0.13	
ICC	0.54	
N_{sleep_clus}	24	
N_{group}	4	
N_{tag}	6	
N_{night}	377	

Observations	1611
Marginal R^2 / Conditional R^2	0.003 / 0.236

Table S3.6. Model output table of the model of the sleep fragmentation during the sleep period. The response variable (sleep fragmentation) is standardized.

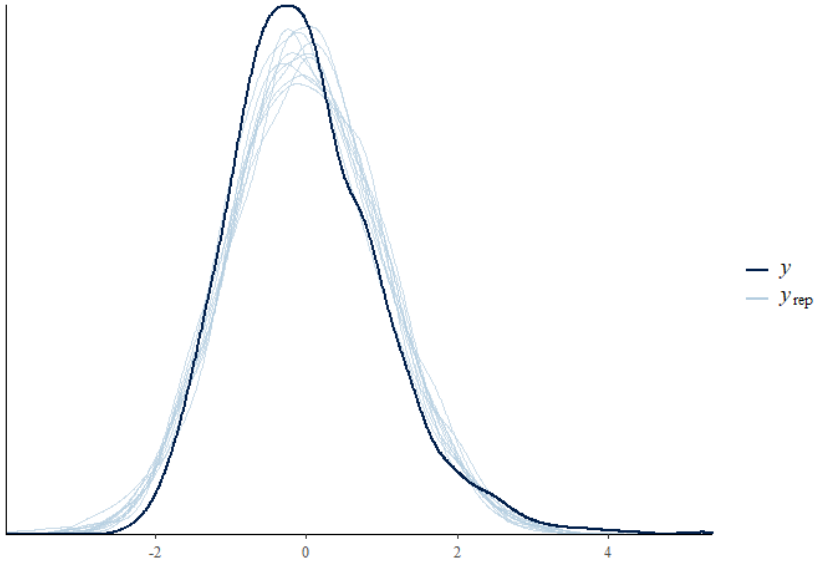

Figure S3.7. Posterior predictive check of the model of the sleep fragmentation during the sleep period. The response variable (sleep fragmentation) is standardized.

	Temporal sleep coordination score (standardized)	
Predictors	*Estimates*	*CI (90%)*
Intercept	0.02	-0.45 – 0.49
Group dyad sleeping at same site	0.18	0.00 – 0.37
Random Effects		
σ^2	0.90	
$\tau_{00\ dyad\_name}$	0.01	
$\tau_{00\ tag\_a}$	0.20	
$\tau_{00\ tag\_b}$	0.13	
ICC	0.27	
N_{tag_a}	5	
N_{tag_b}	5	
N_{dyad_name}	13	
Observations	2621	
Marginal R^2 / Conditional R^2	0.001 / 0.098	

Table S3.7. Model output table of the model of the temporal sleep coordination score between the median sleep site arrival time and median sleep site departure time. The response variable (temporal sleep coordination score) is standardized.

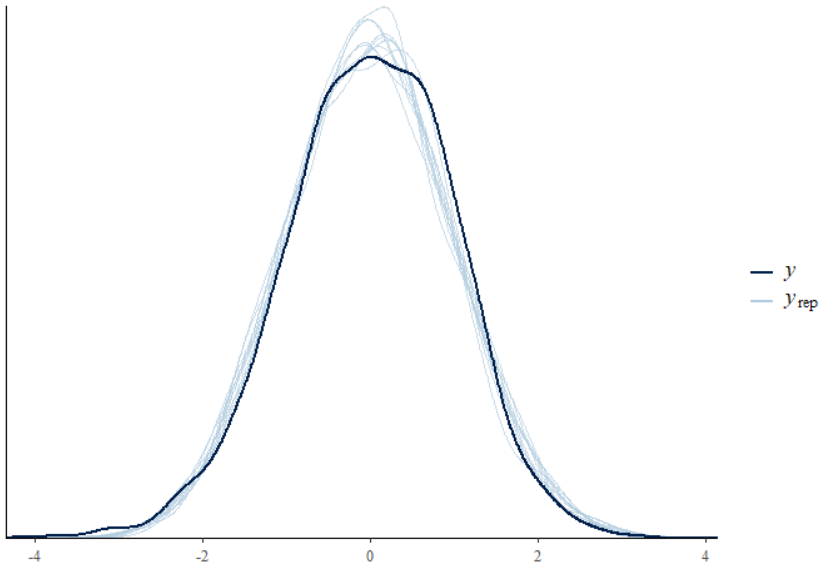

Figure S3.8. Posterior predictive check of the model of the temporal sleep coordination score between the median sleep site arrival time and median sleep site departure time. The response variable (temporal sleep coordination score) is standardized.

	Occurrence of intergroup encounter (binary)	
Predictors	*Log-Odds*	*CI (90%)*
Intercept	-2.64	-5.44 – 0.48
Group dyad coslept night before	2.84	2.25 – 3.47
Random Effects		
σ^2	3.29	
$\tau_{00\ dy\_name}$	6.08	
$\tau_{00\ group1}$	4.15	
$\tau_{00\ group2}$	2.38	
ICC	0.79	
N_{group1}	3	
N_{group2}	3	
N_{dy_name}	6	
Observations	1456	
Marginal R^2 / Conditional R^2	0.080 / 0.252	

Table S3.8. Model output table of the model of the occurrence of an intergroup interaction during the day.

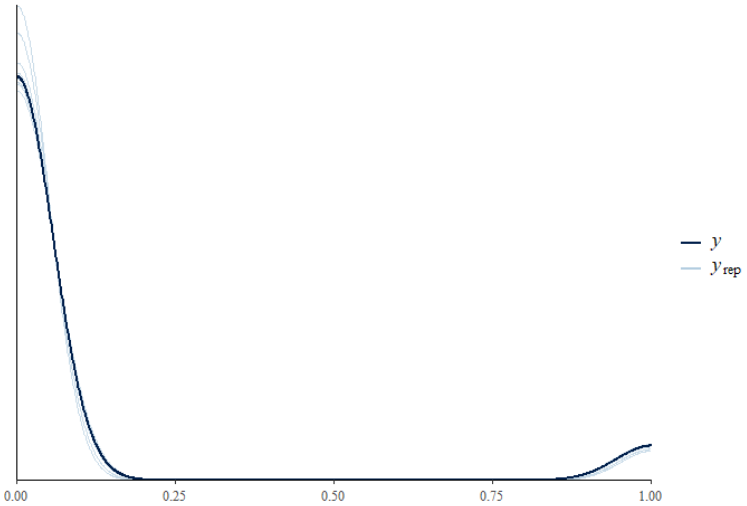

Figure S3.9. Posterior predictive check of the model of the occurrence of an intergroup interaction during the day.

	Occurrence of cohesive movement during intergroup encounter (binary)	
Predictors	*Log-Odds*	*CI (90%)*
Intercept	-1.74	-4.19 – 0.39
Group dyad coslept night before	1.60	0.82 – 2.41
Random Effects		
σ^2	3.29	
$\tau_{00\ dy\_name}$	1.10	
$\tau_{00\ group1}$	1.99	
$\tau_{00\ group2}$	1.72	
ICC	0.59	
N_{group1}	3	
N_{group2}	3	
N_{dy_name}	5	
Observations	115	
Marginal R^2 / Conditional R^2	0.077 / 0.164	

Table S3.9. Model output table of the model of the occurrence of extended cohesive movements, given that an encountered occurred.

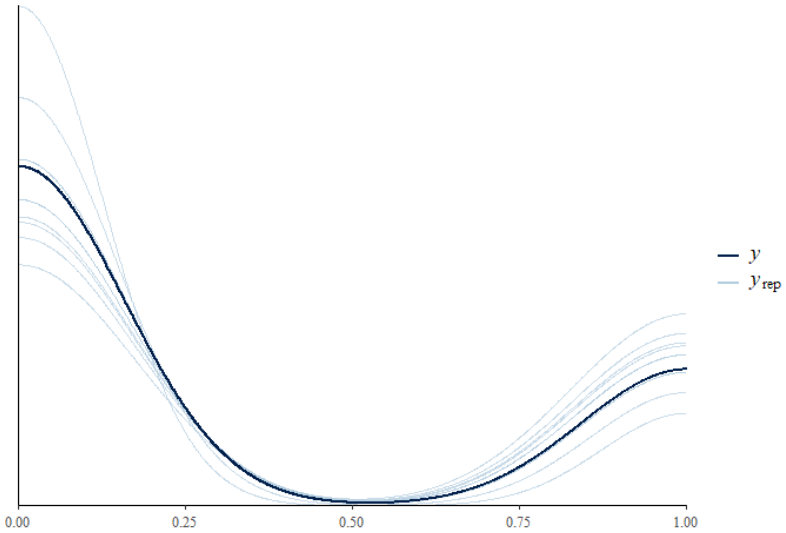

Figure S3.10. Posterior predictive check of the model of the occurrence of extended cohesive movements, given that an encountered occurred.

Conclusion

By investigating sleep in the environment in which it evolved, my dissertation research demonstrates that, despite the critical functions of sleep in maintaining health and survival, sacrificing sleep when in risky environments or when presented with opportunities to develop and maintain social bonds—not only with group-mates but also with individuals from neighboring social groups—may represent an essential adaptation for wild animals. These sleep sacrifices may have important consequences not only for the fitness of an individual, but also for the collective dynamics of a social group and even the social organization of an entire population.

My research reveals the trade-offs that animals face across levels of biological organization when fulfilling their physiological sleep requirement in the wild, and sheds light on the strategies with which they navigate these trade-offs. At the individual level, animals sacrifice investment in sleep when in less familiar—and thus, potentially riskier—locations, regardless of their recent history of sleep and physical exertion (Chapter 1). Within a group, the sleep patterns of individuals both influence and are influenced by the sleep patterns of their group-mates—particularly, socially affiliated group-mates—which causes social disruptions of sleep that decrease sleep quality (Chapters 1 and 2). While socially central individuals disproportionately bear the consequences of these collective dynamics, their loss of sleep may actually reflect a prioritization of investing in the social bonds that are crucial to their fitness (Chapter 2). At the population level, interactions between the members of distinct social groups that occur while sharing a sleep site catalyze tolerant relationships between neighboring groups, but do so at the cost of sleep quality within the shared refuge (Chapter 3). Thus, my dissertation research exposes fundamental interdependencies between an animal's behavioral ecology and its sleep physiology that persist across scales of biological organization.

By demonstrating that complex and dynamic pressures inherent to ecologically and socially relevant contexts play a central role in shaping sleep behavior, my dissertation highlights the importance of studying sleep in the wild. Studies of sleep in the laboratory have emphasized the importance of fulfilling a physiological sleep imperative to reap the benefits that sleep provides (Kitamura et al., 2016). However, the chapters of this dissertation suggest that "sleep need" may be a

flexible concept: the risks and opportunity costs associated with sleep in the wild may be just as important as its benefits in driving variation in sleep patterns.

Further investigation of sleep in ecologically and socially relevant contexts will dramatically improve our understanding of one of the most universal animal behaviors. My dissertation research reveals the trade-offs that wild animals face when investing in sleep. However, understanding the fitness consequences of the strategies with which animals navigate these trade-offs is essential to understanding the role of such trade-offs in shaping the evolutionary trajectory of sleep, as well as its manifestation and variation in the natural world today. How does increased vigilance during the night actually influence the probability of succumbing to predation in unfamiliar habitats? To what extent do animals interact with group-mates during periods of collective wakefulness, and what is the marginal influence of these social interactions on their survival, reproductive output, and the survival of their offspring? How do animals benefit from interacting with individuals in other groups or from tolerant relationships with these groups? What are the physiological costs of sleep sacrifices and how do they affect fitness? When can sleep *not* be sacrificed? The data to explore these crucial next steps may already exist in the multitudes of accelerometry datasets that have been amassed in recent years (Watanabe & Rutz, 2022). Leveraging the tools that I have developed as part of my dissertation research to realize the untapped potential of these existing datasets—as well as those yet to come—could answer these pressing questions, and in doing so, unravel one of biology's greatest mysteries: the evolutionary origin of sleep.

I introduced this dissertation with an account of our own sleep, highlighting that one in three Americans are sleep deprived, and that this deprivation largely arises from the intentional sacrifice of sleep in favor of commitments that require our waking attention (Murphy & Delanty, 2007; Sheehan et al., 2019). My findings reveal that the competing demands on our time that lead to sleep deprivation are not unique to modern, industrialized societies. On the contrary, we have likely grappled with these trade-offs throughout our evolutionary history. As our earliest hominin ancestors moved into their new niche in the expanding savannahs, they likely faced many of the same pressures as those faced by modern baboons (Brain, 1970, 1983; Cerling et al., 2011; Isbell et al., 2018). Thus, they too may have sacrificed sleep to remain vigilant against the diverse and abundant carnivore

megafauna that dominated the early savannahs (Treves & Palmqvist, 2007; Werdelin & Lewis, 2005). They also may have interacted with conspecifics when congregating at shared sleep refuges (Aureli et al., 2008; Willems & van Schaik, 2017), and done so at the cost of sleep. These ecological and social environments of sleep may have further transformed over time, as hominins gained control of fire and began sleeping on the ground (Coolidge & Wynn, 2006; Nunn et al., 2016; Samson & Nunn, 2015). With the transformation of the sleep environment, the pressures within it may have increasingly presented opportunity costs of sleep, tipping the balance between the costs and benefits of investing in sleep. Accordingly, natural selection may have favored the particularly short and intense sleep that modern humans exhibit today (Nunn et al., 2016; Nunn & Samson, 2018; Samson & Nunn, 2015). Thus, understanding how we sleep today and how our sleep will continue to evolve into the future—as we face new demands on our time and new sleep trade-offs—may involve looking to the environment in which sleep evolved, where its adaptive value reflects the complex trade-offs that have shaped its evolution.

References

Almeida, C. M. O. de, & Malheiro, A. (2016). Sleep, immunity and shift workers: A review. *Sleep Science*, *9*(3), 164–168. https://doi.org/10.1016/j.slsci.2016.10.007

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3–4), 227–266.

Altmann, J., Altmann, S., & Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, Papio cynocephalus, in Amboseli National Park, Kenya. *American Journal of Primatology*, *1*(4), 389–399. https://doi.org/10.1002/ajp.1350010404

Altmann, S. A., & Altmann, J. (1970). *Baboon ecology: African field research*. University of Chicago Press, Chicago.

Amlaner, C. J., Phil, D., & Fuller, P. M. (2009). *Basics of sleep guide*. Sleep Research Society.

Ancoli-Israel, S., Cole, R., Alessi, C., Chambers, M., Moorcroft, W., & Pollak, C. P. (2003). The Role of Actigraphy in the Study of Sleep and Circadian Rhythms. *Sleep*, *26*(3), 342–392. https://doi.org/10.1093/sleep/26.3.342

Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. In *Advances in the Study of Behavior* (Vol. 14, pp. 165–229). Elsevier.

Anderson, J. R. (1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *American Journal of Primatology*, *46*(1), 63–75.

Anderson, J. R. (2000). Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews*, *4*(4), 355–373.

Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141261. https://doi.org/10.1098/rspb.2014.1261

Aulsebrook, A. E., Jones, T. M., Rattenborg, N. C., Roth, T. C., & Lesku, J. A. (2016). Sleep Ecophysiology: Integrating Neuroscience and Ecology. *Trends in Ecology & Evolution*, *31*(8), 590–599. https://doi.org/10.1016/j.tree.2016.05.004

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Schaik, C. P. van. (2008). Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Bäckman, J., Andersson, A., Pedersen, L., Sjöberg, S., Tøttrup, A. P., & Alerstam, T. (2017). Actogram analysis of free-flying migratory birds: New perspectives based on acceleration logging. *Journal of Comparative Physiology A*, *203*(6–7), 543–564. https://doi.org/10.1007/s00359-017-1165-9

Barnes, C. M., & Drake, C. L. (2015). Prioritizing Sleep Health: Public Health Policy Recommendations. *Perspectives on Psychological Science*, *10*(6), 733–737. https://doi.org/10.1177/1745691615598509

Barrett, C. E., Noble, P., Hanson, E., Pine, D. S., Winslow, J. T., & Nelson, E. E. (2009). Early adverse rearing experiences alter sleep–wake patterns and plasma cortisol levels in juvenile rhesus monkeys. *Psychoneuroendocrinology*, *34*(7), 1029–1040. https://doi.org/10.1016/j.psyneuen.2009.02.002

Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, *38*(5), 321–329. https://doi.org/10.1007/s002650050248

Basner, M., Fomberstein, K. M., Razavi, F. M., Banks, S., William, J. H., Rosa, R. R., & Dinges, D. F. (2007). American Time Use Survey: Sleep Time and Its Relationship to Waking Activities. *Sleep*, *30*(9), 1085–1095. https://doi.org/10.1093/sleep/30.9.1085

Basner, M., Rao, H., Goel, N., & Dinges, D. F. (2013). Sleep deprivation and neurobehavioral dynamics. *Current Opinion in Neurobiology*, *23*(5), 854–863. https://doi.org/10.1016/j.conb.2013.02.008

Bastuji, H., & García-Larrea, L. (1999). Sleep/wake abnormalities in patients with periodic leg movements during sleep: Factor analysis on data from 24-h ambulatory polygraphy. *Journal of Sleep Research*, *8*(3), 217–223. https://doi.org/10.1046/j.1365-2869.1999.00157.x

Beauchamp, G. (2009). Sleeping gulls monitor the vigilance behaviour of their neighbours. *Biology Letters*, *5*(1), 9–11. https://doi.org/10.1098/rsbl.2008.0490

Beauchamp, G. (2011). Collective waves of sleep in gulls (Larus spp.). *Ethology*, *117*(4), 326–331. https://doi.org/10.1111/j.1439-0310.2011.01875.x

Bednekoff, P. A., & Lima, S. L. (1998). Re–examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1409), 2021–2026. https://doi.org/10.1098/rspb.1998.0535

Behrendt, S., Dimpfl, T., Peter, F. J., & Zimmermann, D. J. (2019). RTransferEntropy—Quantifying information flow between different time series using effective transfer entropy. *SoftwareX*, *10*, 100265. https://doi.org/10.1016/j.softx.2019.100265

Bellman, R., & Kalaba, R. (1959). On adaptive control processes. *IRE Transactions on Automatic Control*, *4*(2), 1–9. https://doi.org/10.1109/TAC.1959.1104847

Ben Simon, E., Rossi, A., Harvey, A. G., & Walker, M. P. (2020). Overanxious and underslept. *Nature Human Behaviour*, *4*(1), 100–110. https://doi.org/10.1038/s41562-019-0754-8

Ben Simon, E., & Walker, M. P. (2018). Sleep loss causes social withdrawal and loneliness. *Nature Communications*, *9*(1), 3146. https://doi.org/10.1038/s41467-018-05377-0

Benoit, T., & Elmarhraoui, A. (2019). *suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase* (R package version 0.5.0) [Computer software]. https://CRAN.R-project.org/package=suncalc

Berger, H. (1931). Uber das EEG des menschen.[On the electroencephalogram of man: Third report]. *Arch Psychiat Nervenkr*, *94*, 16–30.

Bergman, T. J. (2010). Experimental evidence for limited vocal recognition in a wild primate: Implications for the social complexity hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1696), 3045–3053. https://doi.org/10.1098/rspb.2010.0580

Bidner, L. R., Matsumoto-Oda, A., & Isbell, L. A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *American Journal of Primatology*, *80*(12), e22932.

Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, *24*(2), 66–67. https://doi.org/10.1016/j.tree.2008.11.001

Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011a). Social networks and models for collective motion in animals. *Behavioral Ecology and Sociobiology*, *65*(2), 117–130. https://doi.org/10.1007/s00265-010-1111-0

Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011b). The impact of social networks on animal collective motion. *Animal Behaviour*, *82*(1), 29–38. https://doi.org/10.1016/j.anbehav.2011.04.011

Brain, C. K. (1970). New Finds at the Swartkrans Australopithecine Site. *Nature*, *225*(5238), 1112–1119. https://doi.org/10.1038/2251112a0

Brain, C. K. (1983). *The hunters or the hunted?: An introduction to African cave taphonomy*. University of Chicago Press.

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, *85*(4), 807–816. https://doi.org/10.1016/j.anbehav.2013.01.027

Brutcher, R. E., & Nader, M. A. (2013). The relationship between cocaine self-administration and actigraphy-based measures of sleep in adult rhesus monkeys. *Psychopharmacology*, *229*(2), 267–274. https://doi.org/10.1007/s00213-013-3101-1

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Burnham, K., & Anderson, D. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd Edition). Springer.

Busse, C. (1980). Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records*, 15–21.

Buysse, D. J. (2014). Sleep Health: Can We Define It? Does It Matter? *Sleep*, *37*(1), 9–17. https://doi.org/10.5665/sleep.3298

Cacioppo, J. T., Hawkley, L. C., Berntson, G. G., Ernst, J. M., Gibbs, A. C., Stickgold, R., & Hobson, J. A. (2002). Do Lonely Days Invade the Nights? Potential Social Modulation of Sleep Efficiency. *Psychological Science*, *13*(4), 384–387. https://doi.org/10.1111/1467-9280.00469

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, *106*(33), 13850–13853. https://doi.org/10.1073/pnas.0900639106

Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., & Alberts, S. C. (2020). Social bonds, social status and survival in wild baboons: A tale of two sexes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1811), 20190621. https://doi.org/10.1098/rstb.2019.0621

Capellini, I., Barton, R. A., McNamara, P., Preston, B. T., & Nunn, C. L. (2008). Phylogenetic analysis of the ecology and evolution of mammalian sleep. *Evolution: International Journal of Organic Evolution*, *62*(7), 1764–1776.

Capellini, I., Preston, B. T., McNamara, P., Barton, R. A., & Nunn, C. L. (2010). Ecological constraints on mammalian sleep architecture. *Evolution of Sleep: Phylogenetic and Functional Perspectives*, 12–33.

Carter, A. J., Tico, M. T., & Cowlishaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *Elife*, *5*, e13125.

Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., Mace, W., Macharia, A. N., Quade, J., & Remien, C. H. (2011). Woody cover and hominin environments in the past 6 million years. *Nature*, *476*(7358), 51–56. https://doi.org/10.1038/nature10306

Chapman, C. A., Chapman, L. J., & McLaughlin, R. L. (1989). Multiple Central Place Foraging by Spider Monkeys: Travel Consequences of Using Many Sleeping Sites. *Oecologia*, *79*(4), 506–511.

Chen, T., He, T., Benesty, M., Khotilovich, V., Tang, Y., Cho, H., & Chen, K. (2015). Xgboost: Extreme gradient boosting. *R Package Version 0.4-2*, *1*(4), 1–4.

Cheney, D. L., & Seyfarth, R. M. (1977). Behaviour of adult and immature male baboons during inter-group encounters. *Nature*, *269*(5627), 404–406. https://doi.org/10.1038/269404a0

Cheney, D. L., & Seyfarth, R. M. (2008). *Baboon metaphysics: The evolution of a social mind*. University of Chicago Press.

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D., & Silk, J. B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology*, *25*(2), 401–428.

Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2016). Network connections, dyadic bonds and fitness in wild female baboons. *Royal Society Open Science*, *3*(7), 160255.

Childress, M. J., & Herrnkind, W. F. (1997). Den sharing by juvenile Caribbean spiny lobsters (Panulirus argus) in nursery habitat: Cooperation or coincidence? *Marine and Freshwater Research*, *48*(8), 751–758. https://doi.org/10.1071/mf97158

Chowdhury, B., & Shafer, O. T. (2020). Why the young sleep longer. *ELife*, *9*, e56833. https://doi.org/10.7554/eLife.56833

Cirelli, C., & Tononi, G. (2008). Is Sleep Essential? *PLOS Biology*, *6*(8), e216. https://doi.org/10.1371/journal.pbio.0060216

Conradt, L., Krause, J., Couzin, I. D., & Roper, T. J. (2009). "Leading according to need" in self-organizing groups. *The American Naturalist*, *173*(3), 304–312. https://doi.org/10.1086/596532

Conradt, R., Brandenburg, U., Ploch, T., & Peter, J. H. (1997). Actigraphy: Methodological Limits for Evaluation of Sleep Stages and Sleep Structure of Healthy Probands. *Pneumologie (Stuttgart, Germany)*, *51*, 721–724.

Coolidge, F. L., & Wynn, T. G. (2018). *The rise of Homo sapiens: The evolution of modern thinking*. Oxford University Press.

Coolidge, F., & Wynn, T. (2006). The effects of the tree-to-ground sleep transition in the evolution of cognition in early *Homo*. *Before Farming*, *2006*(4), 1–18. https://doi.org/10.3828/bfarm.2006.4.11

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516. https://doi.org/10.1038/nature03236

Cowlishaw, G. (1994). Vulnerability To Predation in Baboon Populations. *Behaviour*, *131*(3–4), 293–304. https://doi.org/10.1163/156853994X00488

Csardi, G., & Nepusz, T. (2005). The Igraph Software Package for Complex Network Research. *InterJournal*, *Complex Systems*, 1695.

Davimes, J. G., Alagaili, A. N., Bhagwandin, A., Bertelsen, M. F., Mohammed, O. B., Bennett, N. C., Manger, P. R., & Gravett, N. (2018). Seasonal variations in sleep of free-ranging Arabian oryx (Oryx leucoryx) under natural hyperarid conditions. *Sleep*, *41*(5). https://doi.org/10.1093/sleep/zsy038

de Souza, L., Benedito-Silva, A. A., Pires, M. L. N., Poyares, D., Tufik, S., & Calil, H. M. (2003). Further Validation of Actigraphy for Sleep Studies. *Sleep*, *26*(1), 81–85. https://doi.org/10.1093/sleep/26.1.81

del Mar Delgado, M., Miranda, M., Alvarez, S. J., Gurarie, E., Fagan, W. F., Penteriani, V., di Virgilio, A., & Morales, J. M. (2018). The importance of individual variation in the dynamics of animal collective movements. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170008. https://doi.org/10.1098/rstb.2017.0008

Devine, J. K., Chinoy, E. D., Markwald, R. R., Schwartz, L. P., & Hursh, S. R. (2021). Validation of Zulu Watch against Polysomnography and Actigraphy for On-Wrist Sleep-Wake Determination and Sleep-Depth Estimation. *Sensors*, *21*(1), 76. https://doi.org/10.3390/s21010076

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D., & Wikelski, M. (2013). The environmental-data automated track annotation (Env-DATA) system: Linking animal tracks with environmental data. *Movement Ecology*, *1*(1), 3. https://doi.org/10.1186/2051-3933-1-3

Drewe, J. A., Madden, J. R., & Pearce, G. P. (2009). The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology*, *63*(9), 1295–1306. https://doi.org/10.1007/s00265-009-0782-x

Drews, H. J., Wallot, S., Brysch, P., Berger-Johannsen, H., Weinhold, S. L., Mitkidis, P., Baier, P. C., Lechinger, J., Roepstorff, A., & Göder, R. (2020). Bed-Sharing in Couples Is Associated With Increased and Stabilized REM Sleep and Sleep-Stage Synchronization. *Frontiers in Psychiatry*, *11*. https://www.frontiersin.org/article/10.3389/fpsyt.2020.00583

Duffield, G. A., & Bull, M. C. (2002). Stable social aggregations in an Australian lizard, Egernia stokesii. *Naturwissenschaften*, *89*(9), 424–427. https://doi.org/10.1007/s00114-002-0346-7

Dunbar, R. I. (1992). Time: A hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, *31*(1), 35–49.

Durmer, J. S., & Dinges, D. F. (2005). Neurocognitive Consequences of Sleep Deprivation. *Seminars in Neurology*, *25*(1), 117–129. https://doi.org/10.1055/s-2005-867080

Eban-Rothschild, A., & Bloch, G. (2012). Social Influences on Circadian Rhythms and Sleep in Insects. In *Advances in Genetics* (Vol. 77, pp. 1–32). Elsevier. https://doi.org/10.1016/B978-0-12-387687-4.00001-5

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R., Strandburg-Peshkin, A., Berger-Wolf, T., Ziebart, B., Brugere, I., Li, J., & Crofoot, M. C. (2016). Both nearest neighbours and long-term affiliates predict individual locations during collective movement in wild baboons. *Scientific Reports*, *6*, 27704.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *The Journal of Wildlife Management*, *69*(4), 1346–1359. https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Finkbeiner, S. D., Briscoe, A. D., & Reed, R. D. (2012). The benefit of being a social butterfly: Communal roosting deters predation. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1739), 2769–2776. https://doi.org/10.1098/rspb.2012.0203

Forrester, T. D., Casady, D. S., & Wittmer, H. U. (2015). Home sweet home: Fitness consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and Sociobiology*, *69*(4), 603–612. https://doi.org/10.1007/s00265-014-1871-z

Frank, M. G. (2020). The Ontogenesis of Mammalian Sleep: Form and Function. *Current Sleep Medicine Reports*. https://doi.org/10.1007/s40675-020-00190-y

Frank, M. G., & Heller, H. C. (2019). The Function(s) of Sleep. In H.-P. Landolt & D.-J. Dijk (Eds.), *Sleep-Wake Neurobiology and Pharmacology* (pp. 3–34). Springer International Publishing. https://doi.org/10.1007/164_2018_140

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1829–1836. https://doi.org/10.1098/rspb.2008.1824

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences*, *107*(46), 19949–19954. https://doi.org/10.1073/pnas.1007997107

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gangwisch, J. E. (2014). A Review of Evidence for the Link Between Sleep Duration and Hypertension. *American Journal of Hypertension*, *27*(10), 1235–1242. https://doi.org/10.1093/ajh/hpu071

Gardner, M. G., Bull, C. M., Fenner, A., Murray, K., & Donnellan, S. C. (2007). Consistent social structure within aggregations of the Australian lizard, Egernia stokesii across seven disconnected rocky outcrops. *Journal of Ethology*, *25*(3), 263–270. https://doi.org/10.1007/s10164-006-0022-z

Gehr, B., Bonnot, N. C., Heurich, M., Cagnacci, F., Ciuti, S., Hewison, A. M., Gaillard, J.-M., Ranc, N., Premier, J., & Vogt, K. (2020). Stay home, stay safe—Site familiarity reduces predation

risk in a large herbivore in two contrasting study sites. *Journal of Animal Ecology*, *89*(6), 1329–1339.

Gordon, A. M., Carrillo, B., & Barnes, C. M. (2021). Sleep and social relationships in healthy populations: A systematic review. *Sleep Medicine Reviews*, *57*, 101428. https://doi.org/10.1016/j.smrv.2021.101428

Gordon, A. M., & Chen, S. (2014). The Role of Sleep in Interpersonal Conflict: Do Sleepless Nights Mean Worse Fights? *Social Psychological and Personality Science*, *5*(2), 168–175. https://doi.org/10.1177/1948550613488952

Gordon, A. M., Mendes, W. B., & Prather, A. A. (2017). The social side of sleep: Elucidating the links between sleep and social processes. *Current Directions in Psychological Science*, *26*(5), 470–475. https://doi.org/10.1177/0963721417712269

Gravett, N., Bhagwandin, A., Sutcliffe, R., Landen, K., Chase, M. J., Lyamin, O. I., Siegel, J. M., & Manger, P. R. (2017). Inactivity/sleep in two wild free-roaming African elephant matriarchs – Does large body size make elephants the shortest mammalian sleepers? *PLOS ONE*, *12*(3), e0171903. https://doi.org/10.1371/journal.pone.0171903

Grueter, C. C., Chapais, B., & Zinner, D. (2012). Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. *International Journal of Primatology*, *33*(5), 1002–1037. https://doi.org/10.1007/s10764-012-9618-z

Grueter, C. C., Qi, X., Li, B., & Li, M. (2017). Multilevel societies. *Current Biology*, *27*(18), R984–R986. https://doi.org/10.1016/j.cub.2017.06.063

Hamilton III, W. J. (1982). Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*, *3*(1–4), 41–53.

Hamilton, W. J., & Watt, K. E. F. (1970). Refuging. *Annual Review of Ecology and Systematics*, *1*(1), 263–286. https://doi.org/10.1146/annurev.es.01.110170.001403

Han, K. S., Kim, L., & Shim, I. (2012). Stress and Sleep Disorder. *Experimental Neurobiology*, *21*(4), 141–150. https://doi.org/10.5607/en.2012.21.4.141

Harel, R., Loftus, J. C., & Crofoot, M. C. (2021). Locomotor compromises maintain group cohesion in baboon troops on the move. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1955), 20210839. https://doi.org/10.1098/rspb.2021.0839

Hasenjager, M. J., Leadbeater, E., & Hoppitt, W. (2021). Detecting and quantifying social transmission using network-based diffusion analysis. *Journal of Animal Ecology*, *90*(1), 8–26. https://doi.org/10.1111/1365-2656.13307

Havmøller, L. W., Loftus, J. C., Havmøller, R. W., Alavi, S. E., Caillaud, D., Grote, M. N., Hirsch, B. T., Tórrez-Herrera, L. L., Kays, R., & Crofoot, M. C. (2021). Arboreal monkeys facilitate foraging of terrestrial frugivores. *Biotropica*, *53*(6), 1685–1697. https://doi.org/10.1111/btp.13017

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006). Prey preferences of the leopard (Panthera pardus). *Journal of Zoology*, *270*(2), 298–313. https://doi.org/10.1111/j.1469-7998.2006.00139.x

Hicks, A. M., & Diamond, L. M. (2011). Don't go to bed angry: Attachment, conflict, and affective and physiological reactivity. *Personal Relationships*, *18*(2), 266–284. https://doi.org/10.1111/j.1475-6811.2011.01355.x

Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A. M., Marlowe, F., Wiessner, P., & Wood, B. (2011). Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. *Science*, *331*(6022), 1286–1289. https://doi.org/10.1126/science.1199071

Hoffmann, K., Coolen, A., Schlumbohm, C., Meerlo, P., & Fuchs, E. (2012). Remote long-term registrations of sleep-wake rhythms, core body temperature and activity in marmoset monkeys. *Behavioural Brain Research*, *235*(2), 113–123. https://doi.org/10.1016/j.bbr.2012.07.033

Holding, B. C., Sundelin, T., Schiller, H., Åkerstedt, T., Kecklund, G., & Axelsson, J. (2020). Sleepiness, sleep duration, and human social activity: An investigation into bidirectionality using longitudinal time-use data. *Proceedings of the National Academy of Sciences*, *117*(35), 21209–21217. https://doi.org/10.1073/pnas.2004535117

Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, *263*(4), 544–555. https://doi.org/10.1016/j.jtbi.2010.01.004

Irwin, M. R. (2019). Sleep and inflammation: Partners in sickness and in health. *Nature Reviews Immunology*, *19*(11), 702–715. https://doi.org/10.1038/s41577-019-0190-z

Isbell, L. A., Bidner, L. R., Crofoot, M. C., Matsumoto-Oda, A., & Farine, D. R. (2017). GPS-identified, low-level nocturnal activity of vervets (Chlorocebus pygerythrus) and olive baboons (Papio anubis) in Laikipia, Kenya. *American Journal of Physical Anthropology*, *164*(1), 203–211.

Isbell, L. A., Bidner, L. R., Van Cleave, E. K., Matsumoto-Oda, A., & Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, *118*, 1–13. https://doi.org/10.1016/j.jhevol.2018.02.003

Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (1990). Costs and benefits of home range shifts among vervet monkeys (Cercopithecus aethiops) in Amboseli National Park, Kenya. *Behavioral Ecology and Sociobiology*, *27*(5), 351–358. https://doi.org/10.1007/BF00164006

Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (1993). Are immigrant vervet monkeys, Cercopithecus aethiops, at greater risk of mortality than residents? *Animal Behaviour*, *45*(4), 729–734. https://doi.org/10.1006/anbe.1993.1087

Isbell, L. A., & Van Vuren, D. (1996). Differential Costs of Locational and Social Dispersal and Their Consequences for Female Group-Living Primates. *Behaviour*, *133*(1/2), 1–36.

Jacobs, A., Watanabe, K., & Petit, O. (2011). Social Structure Affects Initiations of Group Movements but Not Recruitment Success in Japanese Macaques (Macaca fuscata). *International Journal of Primatology*, *32*(6), 1311–1324. https://doi.org/10.1007/s10764-011-9554-3

Johnson, K. T., & Picard, R. W. (2020). Advancing Neuroscience through Wearable Devices. *Neuron*, *108*(1), 8–12. https://doi.org/10.1016/j.neuron.2020.09.030

Jones, S. E., van Hees, V. T., Mazzotti, D. R., Marques-Vidal, P., Sabia, S., van der Spek, A., Dashti, H. S., Engmann, J., Kocevska, D., Tyrrell, J., Beaumont, R. N., Hillsdon, M., Ruth, K. S.,

Tuke, M. A., Yaghootkar, H., Sharp, S. A., Ji, Y., Harrison, J. W., Freathy, R. M., … Wood, A. R. (2019). Genetic studies of accelerometer-based sleep measures yield new insights into human sleep behaviour. *Nature Communications*, *10*(1), 1585. https://doi.org/10.1038/s41467-019-09576-1

Kamau, M. W., Hassell, J. M., Milnes, E. L., Hayek, L.-A. C., Mutinda, M. M., Harel, R., Matsumoto-Oda, A., Yu, J. H., Zimmerman, D., Crofoot, M., & Murray, S. (2021). Point of Care Blood Gas and Electrolyte Analysis in Anesthetized Olive Baboons (Papio anubis) in a Field Setting. *International Journal of Primatology*, *42*(5), 667–681. https://doi.org/10.1007/s10764-021-00241-3

Kanady, J. C., Drummond, S. P. A., & Mednick, S. C. (2011). Actigraphic assessment of a polysomnographic-recorded nap: A validation study. *Journal of Sleep Research*, *20*(1pt2), 214–222. https://doi.org/10.1111/j.1365-2869.2010.00858.x

Karamihalev, S., Flachskamm, C., Eren, N., Kimura, M., & Chen, A. (2019). Social context and dominance status contribute to sleep patterns and quality in groups of freely-moving mice. *Scientific Reports*, *9*(1), 15190. https://doi.org/10.1038/s41598-019-51375-7

Kasaeian, A., Weidenauer, C., Hautzinger, M., & Randler, C. (2019). Reproductive Success, Relationship Orientation, and Sexual Behavior in Heterosexuals: Relationship With Chronotype, Sleep, and Sex. *Evolutionary Psychology*, *17*(3), 1474704919859760. https://doi.org/10.1177/1474704919859760

King, A., & Cowlishaw, G. (2009). All together now: Behavioural synchrony in baboons. *Animal Behaviour*, *78*, 1381–1387. https://doi.org/10.1016/j.anbehav.2009.09.009

King, A. J., Clark, F. E., & Cowlishaw, G. (2011). The dining etiquette of desert baboons: The roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology*, *73*(8), 768–774. https://doi.org/10.1002/ajp.20918

King, A. J., Isaac, N. J., & Cowlishaw, G. (2009). Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons. *Behavioral Ecology*, *20*(5), 1039–1049.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82*(6), 1337–1345.

Kitamura, S., Katayose, Y., Nakazaki, K., Motomura, Y., Oba, K., Katsunuma, R., Terasawa, Y., Enomoto, M., Moriguchi, Y., Hida, A., & Mishima, K. (2016). Estimating individual optimal sleep duration and potential sleep debt. *Scientific Reports*, *6*(1), 35812. https://doi.org/10.1038/srep35812

Kitchen, D., Seyfarth, R., & Cheney, D. (2004). Factors mediating inter-group encounters in savannah baboons (Papio cynocephalus ursinus). *Behaviour*, *141*(2), 197–218. https://doi.org/10.1163/156853904322890816

Knutson, K. L. (2014). Sleep duration, quality, and timing and their associations with age in a community without electricity in haiti. *American Journal of Human Biology*, *26*(1), 80–86. https://doi.org/10.1002/ajhb.22481

Knutson, K. L., Spiegel, K., Penev, P., & Van Cauter, E. (2007). The metabolic consequences of sleep deprivation. *Sleep Medicine Reviews*, *11*(3), 163–178. https://doi.org/10.1016/j.smrv.2007.01.002

Kuhn, H. W. (1955). The Hungarian method for the assignment problem. *Naval Research Logistics Quarterly*, *2*(1–2), 83–97. https://doi.org/10.1002/nav.3800020109

Kuhn, M. (2008). Building Predictive Models in R Using the caret Package. *Journal of Statistical Software*, *28*(5), 1–26. http://dx.doi.org/10.18637/jss.v028.i05

Kummer, H. (1968). *Social organization of Hamadryas baboons. A field study*. University of Chicago Press. https://www.karger.com/Book/Home/217195

Kurina, L. M., Knutson, K. L., Hawkley, L. C., Cacioppo, J. T., Lauderdale, D. S., & Ober, C. (2011). Loneliness Is Associated with Sleep Fragmentation in a Communal Society. *Sleep*, *34*(11), 1519–1526. https://doi.org/10.5665/sleep.1390

Ladha, C., & Hoffman, C. L. (2018). A Combined Approach to Predicting Rest in Dogs Using Accelerometers. *Sensors*, *18*(8), 2649. https://doi.org/10.3390/s18082649

Laland, K. N., & Hoppitt, W. (2013). *Social learning: An introduction to mechanisms, methods, and models.* Princeton University Press.

Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: An analysis of reproductive success from 1989–1999. *American Journal of Physical Anthropology*, *132*(2), 267–277. https://doi.org/10.1002/ajpa.20507

Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: The dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*(4), 449–458. https://doi.org/10.1007/s00265-016-2075-5

Lendrem, D. W. (1983). Sleeping and vigilance in birds. I. Field observations of the mallard (Anas platyrhynchos). *Animal Behaviour*. https://agris.fao.org/agris-search/search.do?recordID=US201302605924

Lesku, J. A., Bark, R. J., Martinez-Gonzalez, D., Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2008). Predator-induced plasticity in sleep architecture in wild-caught Norway rats (Rattus norvegicus). *Behavioural Brain Research*, *189*(2), 298–305. https://doi.org/10.1016/j.bbr.2008.01.006

Lesku, J. A., Meyer, L. C. R., Fuller, A., Maloney, S. K., Dell'Omo, G., Vyssotski, A. L., & Rattenborg, N. C. (2011). Ostriches Sleep like Platypuses. *PLOS ONE*, *6*(8), e23203. https://doi.org/10.1371/journal.pone.0023203

Lesku, J. A., Rattenborg, N. C., Valcu, M., Vyssotski, A. L., Kuhn, S., Kuemmeth, F., Heidrich, W., & Kempenaers, B. (2012). Adaptive Sleep Loss in Polygynous Pectoral Sandpipers. *Science*, *337*(6102), 1654–1658. https://doi.org/10.1126/science.1220939

Lesku, J. A., Roth II, T. C., Amlaner, C. J., & Lima, S. L. (2006). A Phylogenetic Analysis of Sleep Architecture in Mammals: The Integration of Anatomy, Physiology, and Ecology. *The American Naturalist*, *168*(4), 441–453. https://doi.org/10.1086/506973

Leu, S. T., Kappeler, P. M., & Bull, C. M. (2011). The influence of refuge sharing on social behaviour in the lizard Tiliqua rugosa. *Behavioral Ecology and Sociobiology*, *65*(4), 837–847. https://doi.org/10.1007/s00265-010-1087-9

Li, X., Kawachi, I., Buxton, O. M., Haneuse, S., & Onnela, J.-P. (2019). Social network analysis of group position, popularity, and sleep behaviors among U.S. adolescents. *Social Science & Medicine, 232*, 417–426. https://doi.org/10.1016/j.socscimed.2019.05.026

Lima, S. L., Rattenborg, N. C., Lesku, J. A., & Amlaner, C. J. (2005). Sleeping under the risk of predation. *Animal Behaviour*, *70*(4), 723–736. https://doi.org/10.1016/j.anbehav.2005.01.008

Lin, B., Foxfoot, I. R., Miller, C. M., Venkatamaran, V. V., Kerby, J. T., Bechtold, E. K., Kellogg, B. S., Nguyen, N., & Fashing, P. J. (2020). Leopard predation on gelada monkeys at Guassa, Ethiopia. *American Journal of Primatology*, *82*(2), e23098. https://doi.org/10.1002/ajp.23098

Lin, T.-Y., Dollar, P., Girshick, R., He, K., Hariharan, B., & Belongie, S. (2017). *Feature Pyramid Networks for Object Detection*. 2117–2125. https://openaccess.thecvf.com/content_cvpr_2017/html/Lin_Feature_Pyramid_Networks_CVPR_2017_paper.html

Lin, T.-Y., Maire, M., Belongie, S., Hays, J., Perona, P., Ramanan, D., Dollár, P., & Zitnick, C. L. (2014). Microsoft COCO: Common Objects in Context. In D. Fleet, T. Pajdla, B. Schiele, & T. Tuytelaars (Eds.), *Computer Vision – ECCV 2014* (pp. 740–755). Springer International Publishing. https://doi.org/10.1007/978-3-319-10602-1_48

Loftus, J. C., Harel, R., Núñez, C. L., & Crofoot, M. C. (2022). Ecological and social pressures interfere with homeostatic sleep regulation in the wild. *ELife*, *11*, e73695. https://doi.org/10.7554/eLife.73695

Lucchesi, S., Cheng, L., Janmaat, K., Mundry, R., Pisor, A., & Surbeck, M. (2020). Beyond the group: How food, mates, and group size influence intergroup encounters in wild bonobos. *Behavioral Ecology*, *31*(2), 519–532. https://doi.org/10.1093/beheco/arz214

Luyster, F. S., Strollo, P. J., Jr., Zee, P. C., & Walsh, J. K. (2012). Sleep: A Health Imperative. *Sleep*, *35*(6), 727–734. https://doi.org/10.5665/sleep.1846

Lyamin, O. I., Kosenko, P. O., Korneva, S. M., Vyssotski, A. L., Mukhametov, L. M., & Siegel, J. M. (2018). Fur Seals Suppress REM Sleep for Very Long Periods without Subsequent Rebound. *Current Biology*, *28*(12), 2000-2005.e2. https://doi.org/10.1016/j.cub.2018.05.022

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M., & Siegel, J. M. (2008). Cetacean sleep: An unusual form of mammalian sleep. *Neuroscience and Biobehavioral Reviews*, *32*(8), 1451–1484. https://doi.org/10.1016/j.neubiorev.2008.05.023

Mahowald, M. W., & Schenck, C. H. (2005). Insights from studying human sleep disorders. *Nature*, *437*(7063), 1279–1285. https://doi.org/10.1038/nature04287

Malungo, I. B., Gravett, N., Bhagwandin, A., Davimes, J. G., & Manger, P. R. (2021). Sleep in two free-roaming blue wildebeest (Connochaetes taurinus), with observations on the agreement of polysomnographic and actigraphic techniques. *IBRO Neuroscience Reports*, *10*, 142–152. https://doi.org/10.1016/j.ibneur.2021.02.005

Markham, A. C., Alberts, S. C., & Altmann, J. (2016). Haven for the night: Sleeping site selection in a wild primate. *Behavioral Ecology*, *27*(1), 29–35.

Markham, A. C., Guttal, V., Alberts, S. C., & Altmann, J. (2013). When good neighbors don't need fences: Temporal landscape partitioning among baboon social groups. *Behavioral Ecology and Sociobiology*, *67*(6), 875–884. https://doi.org/10.1007/s00265-013-1510-0

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2015). Social effects on foraging behavior and success depend on local environmental conditions. *Ecology and Evolution*, *5*(2), 475–492.

Martin, J. K., & Martin, A. A. (2007). Resource distribution influences mating system in the bobuck (Trichosurus cunninghami: Marsupialia). *Oecologia*, *154*(1), 227–236. https://doi.org/10.1007/s00442-007-0823-y

McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: Fitness-related benefits of social bonds. *Animal Behaviour*, *126*, 101–106. https://doi.org/10.1016/j.anbehav.2017.02.002

Meadows, R., Arber, S., Venn, S., Hislop, J., & Stanley, N. (2009). Exploring the Interdependence of Couples' Rest-Wake Cycles: An Actigraphic Study. *Chronobiology International*, *26*(1), 80–92. https://doi.org/10.1080/07420520802678452

Mednick, S. C., Christakis, N. A., & Fowler, J. H. (2010). The Spread of Sleep Loss Influences Drug Use in Adolescent Social Networks. *PLOS ONE*, *5*(3), e9775. https://doi.org/10.1371/journal.pone.0009775

Miller, P. J. O., Aoki, K., Rendell, L. E., & Amano, M. (2008). Stereotypical resting behavior of the sperm whale. *Current Biology*, *18*(1), R21–R23. https://doi.org/10.1016/j.cub.2007.11.003

Mitani, Y., Andrews, R. D., Sato, K., Kato, A., Naito, Y., & Costa, D. P. (2010). Three-dimensional resting behaviour of northern elephant seals: Drifting like a falling leaf. *Biology Letters*, *6*(2), 163–166. https://doi.org/10.1098/rsbl.2009.0719

Mochida, K., & Nishikawa, M. (2014). Sleep duration is affected by social relationships among sleeping partners in wild Japanese macaques. *Behavioural Processes*, *103*, 102–104. https://doi.org/10.1016/j.beproc.2013.10.010

Mohanty, N. P., Wagener, C., Herrel, A., & Thaker, M. (2022). The ecology of sleep in non-avian reptiles. *Biological Reviews*, *97*(2), 505–526. https://doi.org/10.1111/brv.12808

Mong, J. A., & Cusmano, D. M. (2016). Sex differences in sleep: Impact of biological sex and sex steroids. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1688), 20150110. https://doi.org/10.1098/rstb.2015.0110

Mullington, J. M., Haack, M., Toth, M., Serrador, J. M., & Meier-Ewert, H. K. (2009). Cardiovascular, Inflammatory, and Metabolic Consequences of Sleep Deprivation. *Progress in Cardiovascular Diseases*, *51*(4), 294–302. https://doi.org/10.1016/j.pcad.2008.10.003

Murphy, K., & Delanty, N. (2007). Sleep deprivation: A clinical perspective. *Sleep and Biological Rhythms*, *5*(1), 2–14. https://doi.org/10.1111/j.1479-8425.2006.00251.x

Noser, R., Gygax, L., & Tobler, I. (2003). Sleep and social status in captive gelada baboons (Theropithecus gelada). *Behavioural Brain Research*, *147*(1), 9–15. https://doi.org/10.1016/S0166-4328(03)00111-6

Nunn, C. L., & Samson, D. R. (2018). Sleep in a comparative context: Investigating how human sleep differs from sleep in other primates. *American Journal of Physical Anthropology*, *166*(3), 601–612. https://doi.org/10.1002/ajpa.23427

Nunn, C. L., Samson, D. R., & Krystal, A. D. (2016). Shining evolutionary light on human sleep and sleep disorders. *Evolution, Medicine, and Public Health*, *2016*(1), 227–243. https://doi.org/10.1093/emph/eow018

O'Brien, T. G., & Kinnaird, M. F. (2011). Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. *Ecological Applications*, *21*(8), 2908–2916.

Ohayon, M. M., Carskadon, M. A., Guilleminault, C., & Vitiello, M. V. (2004). Meta-Analysis of Quantitative Sleep Parameters From Childhood to Old Age in Healthy Individuals: Developing Normative Sleep Values Across the Human Lifespan. *Sleep*, *27*(7), 1255–1273. https://doi.org/10.1093/sleep/27.7.1255

Olds, T., Blunden, S., Petkov, J., & Forchino, F. (2010). The relationships between sex, age, geography and time in bed in adolescents: A meta-analysis of data from 23 countries. *Sleep Medicine Reviews*, *14*(6), 371–378. https://doi.org/10.1016/j.smrv.2009.12.002

Packer, C. (1979). Male dominance and reproductive activity in Papio anubis. *Animal Behaviour*, *27*, 37–45. https://doi.org/10.1016/0003-3472(79)90127-1

Pankhurst, F. P., & Home, J. A. (1994). The Influence of Bed Partners on Movement During Sleep. *Sleep*, *17*(4), 308–315. https://doi.org/10.1093/sleep/17.4.308

Papageorgiou, D., Christensen, C., Gall, G. E. C., Klarevas-Irby, J. A., Nyaguthii, B., Couzin, I. D., & Farine, D. R. (2019). The multilevel society of a small-brained bird. *Current Biology*, *29*(21), R1120–R1121. https://doi.org/10.1016/j.cub.2019.09.072

Papageorgiou, D., & Farine, D. R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Science Advances*, *6*(48), eaba5881. https://doi.org/10.1126/sciadv.aba5881

Paszke, A., Gross, S., Massa, F., Lerer, A., Bradbury, J., Chanan, G., Killeen, T., Lin, Z., Gimelshein, N., Antiga, L., Desmaison, A., Kopf, A., Yang, E., DeVito, Z., Raison, M., Tejani, A., Chilamkurthy, S., Steiner, B., Fang, L., … Chintala, S. (2019). PyTorch: An Imperative Style, High-Performance Deep Learning Library. *Advances in Neural Information Processing Systems*, *32*.

https://proceedings.neurips.cc/paper/2019/hash/bdbca288fee7f92f2bfa9f7012727740-Abstract.html

Patel, S. I., Miller, B. W., Kosiorek, H. E., Parish, J. M., Lyng, P. J., & Krahn, L. E. (2017). The Effect of Dogs on Human Sleep in the Home Sleep Environment. *Mayo Clinic Proceedings*, *92*(9), 1368–1372. https://doi.org/10.1016/j.mayocp.2017.06.014

Peterson, R. O., Jacobs, A. K., Drummer, T. D., Mech, L. D., & Smith, D. W. (2002). Leadership behavior in relation to dominance and reproductive status in gray wolves, Canis lupus. *Canadian Journal of Zoology*, *80*(8), 1405–1412. https://doi.org/10.1139/z02-124

Pons, P., & Latapy, M. (2005). Computing communities in large networks using random walks (long version). *ArXiv:Physics/0512106*. http://arxiv.org/abs/physics/0512106

Prather, A. A., Bogdan, R., & Ahmad R. Hariri, P. (2013). Impact of Sleep Quality on Amygdala Reactivity, Negative Affect, and Perceived Stress. *Psychosomatic Medicine*, *75*(4), 350–358. https://doi.org/10.1097/PSY.0b013e31828ef15b

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L., Gleiss, A. C., & Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PloS One*, *7*(2), e31187.

Qin, D.-D., Feng, S.-F., Zhang, F.-Y., Wang, N., Sun, W.-J., Zhou, Y., Xiong, T.-F., Xu, X.-L., Yang, X.-T., Zhang, X., Zhu, X., Hu, X.-T., Xiong, L., Liu, Y., & Chen, Y.-C. (2020). Potential use of actigraphy to measure sleep in monkeys: Comparison with behavioral analysis from videography. *Zoological Research*, *41*(4), 437–443. https://doi.org/10.24272/j.issn.2095-8137.2020.056

R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing* (4.0.5) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Radwan, B., Jansen, G., & Chaudhury, D. (2021). Abnormal Sleep Signals Vulnerability to Chronic Social Defeat Stress. *Frontiers in Neuroscience*, *14*. https://www.frontiersin.org/article/10.3389/fnins.2020.610655

Rattenborg, N. C., de la Iglesia, H. O., Kempenaers, B., Lesku, J. A., Meerlo, P., & Scriba, M. F. (2017). Sleep research goes wild: New methods and approaches to investigate the ecology, evolution and functions of sleep. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1734), 20160251.

Rattenborg, N. C., Lima, S. L., & Amlaner, C. J. (1999a). Half-awake to the risk of predation. *Nature*, *397*(6718), 397–398. https://doi.org/10.1038/17037

Rattenborg, N. C., Lima, S. L., & Amlaner, C. J. (1999b). Facultative control of avian unihemispheric sleep under the risk of predation. *Behavioural Brain Research*, *105*(2), 163–172. https://doi.org/10.1016/S0166-4328(99)00070-4

Rattenborg, N. C., Voirin, B., Cruz, S. M., Tisdale, R., Dell'Omo, G., Lipp, H.-P., Wikelski, M., & Vyssotski, A. L. (2016). Evidence that birds sleep in mid-flight. *Nature Communications*, *7*(1), 12468. https://doi.org/10.1038/ncomms12468

Rattenborg, N. C., Voirin, B., Vyssotski, A. L., Kays, R. W., Spoelstra, K., Kuemmeth, F., Heidrich, W., & Wikelski, M. (2008). Sleeping outside the box: Electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biology Letters*, *4*(4), 402–405. https://doi.org/10.1098/rsbl.2008.0203

Ray, J. C., & Sapolsky, R. M. (1992). Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *American Journal of Primatology*, *28*(4), 231–250.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Rechtschaffen, A., & Bergmann, B. M. (2002). Sleep deprivation in the rat: An update of the 1989 paper. *Sleep*, *25*(1), 18–24. https://doi.org/10.1093/sleep/25.1.18

Reinhardt, K. D. (2020). Wild primate sleep: Understanding sleep in an ecological context. *Current Opinion in Physiology*, *15*, 238–244. https://doi.org/10.1016/j.cophys.2020.04.002

Reinhardt, K. D., Vyazovskiy, V. V., Hernandez-Aguilar, R. A., Imron, M. A., & Nekaris, K. A.-I. (2019). Environment shapes sleep patterns in a wild nocturnal primate. *Scientific Reports*, *9*(1), 9939. https://doi.org/10.1038/s41598-019-45852-2

Ren, S., He, K., Girshick, R., & Sun, J. (2016). Faster R-CNN: Towards Real-Time Object Detection with Region Proposal Networks. *ArXiv:1506.01497 [Cs]*. http://arxiv.org/abs/1506.01497

Reyes, K. R., Patel, U. A., Nunn, C. L., & Samson, D. R. (2021). Gibbon sleep quantified: The influence of lunar phase and meteorological variables on activity in Hylobates moloch and Hylobates pileatus. *Primates*, *62*(5), 749–759. https://doi.org/10.1007/s10329-021-00920-y

Riehl, C., & Strong, M. J. (2018). Stable social relationships between unrelated females increase individual fitness in a cooperative bird. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1876), 20180130. https://doi.org/10.1098/rspb.2018.0130

Robbins, R., Jean-Louis, G., Gallagher, R. A., Hale, L., Branas, C. C., Gooneratne, N., Alfonso-Miller, P., Perlis, M., & Grandner, M. A. (2019). Examining social capital in relation to sleep duration, insomnia, and daytime sleepiness. *Sleep Medicine*, *60*, 165–172. https://doi.org/10.1016/j.sleep.2019.03.019

Robinson, E. J. H., & Barker, J. L. (2017). Inter-group cooperation in humans and other animals. *Biology Letters*, *13*(3), 20160793. https://doi.org/10.1098/rsbl.2016.0793

Roehrs, T., Kapke, A., Roth, T., & Breslau, N. (2006). Sex differences in the polysomnographic sleep of young adults: A community-based study. *Sleep Medicine*, *7*(1), 49–53. https://doi.org/10.1016/j.sleep.2005.05.008

Rosekind, M. R., Gregory, K. B., Mallis, M. M., Brandt, S. L., Seal, B., & Lerner, D. (2010). The Cost of Poor Sleep: Workplace Productivity Loss and Associated Costs. *Journal of Occupational and Environmental Medicine*, *52*(1), 91–98.

Roth, T. C., Rattenborg, N. C., & Pravosudov, V. V. (2010). The ecological relevance of sleep: The trade-off between sleep, memory and energy conservation. *Philosophical Transactions of the*

Royal Society B: Biological Sciences, *365*(1542), 945–959. https://doi.org/10.1098/rstb.2009.0209

Rubenstein, D. I., & Hack, M. (2004). Natural and sexual selection and the evolution of multi-level societies: Insights from zebras with comparisons to primates. *Sexual Selection in Primates: New and Comparative Perspectives*, 266–279.

Samson, D. R. (2021). Taking the sleep lab to the field: Biometric techniques for quantifying sleep and circadian rhythms in humans. *American Journal of Human Biology*, *33*(6), e23541. https://doi.org/10.1002/ajhb.23541

Samson, D. R., Bray, J., & Nunn, C. L. (2018). The cost of deep sleep: Environmental influences on sleep regulation are greater for diurnal lemurs. *American Journal of Physical Anthropology*, *166*(3), 578–589. https://doi.org/10.1002/ajpa.23455

Samson, D. R., Crittenden, A. N., Mabulla, I. A., Mabulla, A. Z. P., & Nunn, C. L. (2017). Chronotype variation drives night-time sentinel-like behaviour in hunter–gatherers. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1858), 20170967. https://doi.org/10.1098/rspb.2017.0967

Samson, D. R., & Nunn, C. L. (2015). Sleep intensity and the evolution of human cognition. *Evolutionary Anthropology: Issues, News, and Reviews*, *24*(6), 225–237. https://doi.org/10.1002/evan.21464

Sanford, L. D., Suchecki, D., & Meerlo, P. (2015). Stress, Arousal, and Sleep. In P. Meerlo, R. M. Benca, & T. Abel (Eds.), *Sleep, Neuronal Plasticity and Brain Function* (pp. 379–410). Springer. https://doi.org/10.1007/7854_2014_314

Sanford, L., Suchecki, D., & Meerlo, P. (2014). Stress, Arousal, and Sleep. *Current Topics in Behavioral Neurosciences*, *25*. https://doi.org/10.1007/7854_2014_314

Sapolsky, R. M. (1983). Endocrine aspects of social instability in the olive baboon (Papio anubis). *American Journal of Primatology*, *5*(4), 365–379. https://doi.org/10.1002/ajp.1350050406

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques. *Current Biology*, *20*(24), 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058

Scriba, M. F., Ducrest, A.-L., Henry, I., Vyssotski, A. L., Rattenborg, N. C., & Roulin, A. (2013). Linking melanism to brain development: Expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny. *Frontiers in Zoology*, *10*(1), 42. https://doi.org/10.1186/1742-9994-10-42

Seeman, T. E. (1996). Social ties and health: The benefits of social integration. *Annals of Epidemiology*, *6*(5), 442–451. https://doi.org/10.1016/S1047-2797(96)00095-6

Sellers, W. I., & Crompton, R. H. (2004). Automatic Monitoring of Primate Locomotor Behaviour Using Accelerometers. *Folia Primatologica*, *75*(4), 279–293. https://doi.org/10.1159/000078939

Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour*, *24*(4), 917–938. https://doi.org/10.1016/S0003-3472(76)80022-X

Shambroom, J. R., Fábregas, S. E., & Johnstone, J. (2012). Validation of an automated wireless system to monitor sleep in healthy adults. *Journal of Sleep Research*, *21*(2), 221–230. https://doi.org/10.1111/j.1365-2869.2011.00944.x

Sheehan, C. M., Frochen, S. E., Walsemann, K. M., & Ailshire, J. A. (2019). Are U.S. adults reporting less sleep?: Findings from sleep duration trends in the National Health Interview Survey, 2004-2017. *Sleep*, *42*(2). https://doi.org/10.1093/sleep/zsy221

Sick, C., Carter, A. J., Marshall, H. H., Knapp, L. A., Dabelsteen, T., & Cowlishaw, G. (2014). Evidence for varying social strategies across the day in chacma baboons. *Biology Letters*, *10*(7), 20140249.

Siegel, J. M. (2008). Do all animals sleep? *Trends in Neurosciences*, *31*(4), 208–213.

Silk, J. B. (2003). Social Bonds of Female Baboons Enhance Infant Survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2009). The benefits of social capital: Close social

bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3099–3104. https://doi.org/10.1098/rspb.2009.0681

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology*, *20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Smeltzer, E. A., Stead, S. M., Li, M. F., Samson, D., Kumpan, L. T., & Teichroeb, J. A. (2022). Social sleepers: The effects of social status on sleep in terrestrial mammals. *Hormones and Behavior*, *143*, 105181. https://doi.org/10.1016/j.yhbeh.2022.105181

Snyder, F. (1966). Toward an evolutionary theory of dreaming. *American Journal of Psychiatry*, *123*, 121–136.

Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012). Defining Higher Levels in the Multilevel Societies of Geladas (Theropithecus gelada). *International Journal of Primatology*, *33*(5), 1054–1068. https://doi.org/10.1007/s10764-012-9584-5

Spiegel, O., Leu, S. T., Sih, A., & Bull, C. M. (2016). Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods in Ecology and Evolution*, *7*(8), 971–979. https://doi.org/10.1111/2041-210X.12553

Spoormaker, V. I., & Montgomery, P. (2008). Disturbed sleep in post-traumatic stress disorder: Secondary symptom or core feature? *Sleep Medicine Reviews*, *12*(3), 169–184. https://doi.org/10.1016/j.smrv.2007.08.008

Sri Kantha, S., & Suzuki, J. (2006). Sleep quantitation in common marmoset, cotton top tamarin and squirrel monkey by non-invasive actigraphy. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *144*(2), 203–210. https://doi.org/10.1016/j.cbpa.2006.02.043

Stammbach, E. (2008). Desert, Forest and Montane Baboons: Multilevel-Societies. In *Primate societies* (pp. 112–120). University of Chicago Press.

Steiger, A., & Kimura, M. (2010). Wake and sleep EEG provide biomarkers in depression. *Journal of Psychiatric Research*, *44*(4), 242–252. https://doi.org/10.1016/j.jpsychires.2009.08.013

Steinmeyer, C., Schielzeth, H., Mueller, J. C., & Kempenaers, B. (2010). Variation in sleep behaviour in free-living blue tits, Cyanistes caeruleus: Effects of sex, age and environment. *Animal Behaviour*, *80*(5), 853–864. https://doi.org/10.1016/j.anbehav.2010.08.005

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature*, *437*(7063), 1272–1278.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*(6241), 1358–1361.

Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *ELife*, *6*, e19505. https://doi.org/10.7554/eLife.19505

Strandburg-Peshkin, A., Papageorgiou, D., Crofoot, M. C., & Farine, D. R. (2018). Inferring influence and leadership in moving animal groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170006. https://doi.org/10.1098/rstb.2017.0006

Strauss, E. D., & Shizuka, D. (2022). The ecology of wealth inequality in animal societies. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974), 20220500. https://doi.org/10.1098/rspb.2022.0500

Stuber, E. F., Dingemanse, N. J., Kempenaers, B., & Mueller, J. C. (2015). Sources of intraspecific variation in sleep behaviour of wild great tits. *Animal Behaviour*, *106*, 201–221. https://doi.org/10.1016/j.anbehav.2015.05.025

Stuber, E. F., Grobis, M. M., Abbey-Lee, R., Kempenaers, B., Mueller, J. C., & Dingemanse, N. J. (2014). Perceived predation risk affects sleep behaviour in free-living great tits, Parus major. *Animal Behaviour*, *98*, 157–165. https://doi.org/10.1016/j.anbehav.2014.10.010

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D., & Aureli, F. (2011). Collective decision-making and fission–fusion dynamics: A conceptual framework. *Oikos*, *120*(11), 1608–1617. https://doi.org/10.1111/j.1600-0706.2011.19685.x

Sueur, C., Petit, O., & Deneubourg, J. L. (2009). Selective mimetism at departure in collective movements of Macaca tonkeana: An experimental and theoretical approach. *Animal Behaviour*, *78*(5), 1087–1095. https://doi.org/10.1016/j.anbehav.2009.07.029

Suzuki, M., Nakayama, M., Ando, K. B., Arima, S., Nakamura, Y., Yokota, M., & Murakami, S. (2018). Sleep Disturbance and Hyperactivity Detected by Actigraphy in Rats with Allergic Rhinitis or Attention-Deficit Hyperactivity Disorder. *The Tohoku Journal of Experimental Medicine*, *246*(2), 65–71. https://doi.org/10.1620/tjem.246.65

Taheri, S. (2006). The link between short sleep duration and obesity: We should recommend more sleep to prevent obesity. *Archives of Disease in Childhood*, *91*(11), 881–884. https://doi.org/10.1136/adc.2005.093013

Takahashi, M. (2012). Prioritizing sleep for healthy work schedules. *Journal of Physiological Anthropology*, *31*(1), 6. https://doi.org/10.1186/1880-6805-31-6

Tamaki, M., Bang, J. W., Watanabe, T., & Sasaki, Y. (2016). Night Watch in One Brain Hemisphere during Sleep Associated with the First-Night Effect in Humans. *Current Biology*, *26*(9), 1190–1194. https://doi.org/10.1016/j.cub.2016.02.063

Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, *126*, 31–40. https://doi.org/10.1016/j.anbehav.2017.01.017

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

Treves, A., & Palmqvist, P. (2007). Reconstructing Hominin Interactions with Mammalian Carnivores (6.0–1.8 Ma). In S. L. Gursky & K. A. I. Nekaris (Eds.), *Primate Anti-Predator Strategies* (pp. 355–381). Springer US. https://doi.org/10.1007/978-0-387-34810-0_17

Troxel, W. M. (2010). It's More than Sex: Exploring the Dyadic Nature of Sleep and Implications for Health. *Psychosomatic Medicine*, *72*(6), 578–586. https://doi.org/10.1097/PSY.0b013e3181de7ff8

Troxel, W. M., Robles, T. F., Hall, M., & Buysse, D. J. (2007). Marital quality and the marital bed: Examining the covariation between relationship quality and sleep. *Sleep Medicine Reviews*, *11*(5), 389–404. https://doi.org/10.1016/j.smrv.2007.05.002

van der Helm, E., Gujar, N., & Walker, M. P. (2010). Sleep Deprivation Impairs the Accurate Recognition of Human Emotions. *Sleep*, *33*(3), 335–342. https://doi.org/10.1093/sleep/33.3.335

van Hees, V. T., Sabia, S., Anderson, K. N., Denton, S. J., Oliver, J., Catt, M., Abell, J. G., Kivimäki, M., Trenell, M. I., & Singh-Manoux, A. (2015). A novel, open access method to assess sleep duration using a wrist-worn accelerometer. *PloS One*, *10*(11), e0142533.

van Hees, V. T., Sabia, S., Jones, S. E., Wood, A. R., Anderson, K. N., Kivimäki, M., Frayling, T. M., Pack, A. I., Bucan, M., Trenell, M. I., Mazzotti, D. R., Gehrman, P. R., Singh-Manoux, B. A., & Weedon, M. N. (2018). Estimating sleep parameters using an accelerometer without sleep diary. *Scientific Reports*, *8*(1), 12975. https://doi.org/10.1038/s41598-018-31266-z

Voirin, B., Scriba, M. F., Martinez-Gonzalez, D., Vyssotski, A. L., Wikelski, M., & Rattenborg, N. C. (2014). Ecology and Neurophysiology of Sleep in Two Wild Sloth Species. *Sleep*, *37*(4), 753–761. https://doi.org/10.5665/sleep.3584

Vyazovskiy, V. V. (2015). Sleep, recovery, and metaregulation: Explaining the benefits of sleep. *Nature and Science of Sleep*, *7*, 171–184. https://doi.org/10.2147/NSS.S54036

Walker, M. P. (2009). The Role of Sleep in Cognition and Emotion. *Annals of the New York Academy of Sciences*, *1156*(1), 168–197. https://doi.org/10.1111/j.1749-6632.2009.04416.x

Ward, A., & Webster, M. (2016). *Sociality: The behaviour of group-living animals*.

Watanabe, Y. Y., & Rutz, C. (2022). Accelerometer-based analyses of animal sleep patterns. *ELife*, *11*, e77349. https://doi.org/10.7554/eLife.77349

Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*(7812), 337–340. https://doi.org/10.1038/d41586-020-01751-5

Werdelin, L., & Lewis, M. E. (2005). Plio-Pleistocene Carnivora of eastern Africa: Species richness and turnover patterns. *Zoological Journal of the Linnean Society*, *144*(2), 121–144.

Willems, E. P., & van Schaik, C. P. (2017). The social organization of Homo ergaster: Inferences from anti-predator responses in extant primates. *Journal of Human Evolution*, *109*, 11–21. https://doi.org/10.1016/j.jhevol.2017.05.003

Williams, H. J., Shipley, J. R., Rutz, C., Wikelski, M., Wilkes, M., & Hawkes, L. A. (2021). Future trends in measuring physiology in free-living animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1831), 20200230. https://doi.org/10.1098/rstb.2020.0230

Winnebeck, E. C., Fischer, D., Leise, T., & Roenneberg, T. (2018). Dynamics and Ultradian Structure of Human Sleep in Real Life. *Current Biology*, *28*(1), 49-59.e5. https://doi.org/10.1016/j.cub.2017.11.063

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*(1), 13361. https://doi.org/10.1038/ncomms13361

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wrangham, R., & Carmody, R. (2010). Human adaptation to the control of fire. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(5), 187–199. https://doi.org/10.1002/evan.20275

Wright, A. J., Akamatsu, T., Mouritsen, K. N., Sveegaard, S., Dietz, R., & Teilmann, J. (2017). Silent porpoise: Potential sleeping behaviour identified in wild harbour porpoises. *Animal Behaviour*, *133*, 211–222. https://doi.org/10.1016/j.anbehav.2017.09.015

Wrona, F. J., & Dixon, R. J. (1991). Group size and predation risk: A field analysis of encounter and dilution effects. *The American Naturalist*, *137*(2), 186–201.

Wu, Y., Kirillov, A., Massa, F., Lo, W.-Y., & Girshick, R. (2019). *Detectron2*. https://github.com/facebookresearch/detectron2

Xie, L., Kang, H., Xu, Q., Chen, M. J., Liao, Y., Thiyagarajan, M., O'Donnell, J., Christensen, D. J., Nicholson, C., Iliff, J. J., Takano, T., Deane, R., & Nedergaard, M. (2013). Sleep Drives Metabolite Clearance from the Adult Brain. *Science*, *342*(6156), 373–377. https://doi.org/10.1126/science.1241224

Yoder, J. M., Marschall, E. A., & Swanson, D. A. (2004). The cost of dispersal: Predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, *15*(3), 469–476.

Zhang, P., Li, B., Watanabe, K., & Qi, X. (2011). Sleeping cluster patterns and retiring behaviors during winter in a free-ranging band of the Sichuan snub-nosed monkey. *Primates*, *52*(3), 221–228. https://doi.org/10.1007/s10329-011-0241-y

Zhdanova, I. V., Geiger, D. A., Schwagerl, A. L., Leclair, O. U., Killiany, R., Taylor, J. A., Rosene, D. L., Moss, M. B., & Madras, B. K. (2002). Melatonin promotes sleep in three species of diurnal nonhuman primates. *Physiology & Behavior*, *75*(4), 523–529. https://doi.org/10.1016/S0031-9384(02)00654-6

Zielinski, M. R., McKenna, J. T., & McCarley, R. W. (2016). Functions and Mechanisms of Sleep. *AIMS Neuroscience*, *3*(1), 67–104. https://doi.org/10.3934/Neuroscience.2016.1.67