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

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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 studies of sleep have been conducted in highly controlled settings, disconnected from the ecological and social context that may exert pressures on sleep patterns in conflict with homeostatic regulation. Using tri-axial accelerometry and GPS to track the sleep patterns of a group of wild baboons (*Papio anubis*) at multiple temporal and spatial scales, 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 much they had slept the prior night or how much they had physically exerted themselves the preceding day. Moreover, 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 reflect 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 every 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 Rattenborg et al., 2016),

93   and investing in sleep when environmental forces render vigilance and activity particularly important

94   may impose substantial costs to wild animals. In addition to preventing animals from foraging,

95   searching for mating opportunities, defending territories, and caring for young, sleep leaves animals in

96   a state of extreme inattention, and thus highly vulnerable to their predators (Lima et al., 2005). The

97   evolution of sleep and its manifestation in the wild may therefore be driven by a complex balance

98   between the physiological need for sleep and ecological costs imposed on sleeping animals.

99   For gregarious animals, the balance between the costs and benefits of sleep may be further

100   modulated by the social environment. However, even the most basic aspects of sleeping with

101   conspecifics, such as whether the social context facilitates or constrains sleep, remain unknown

102   (Karamihalev et al., 2019). Sleeping in a social context could alter the costs of sleep – the sentinel

103   hypothesis suggests that staggering the timing of sleep bouts in a group can collectively maintain both

104   high quality sleep and high levels of anti-predator vigilance (Samson et al., 2017; Snyder, 1966).

105   Sleeping in a group may therefore facilitate an individual's ability to fulfill its physiological

106   requirements for sleep by reducing the risk of doing so. Alternatively, social dynamics may actually

107   inhibit investment in sleep. Sleep may present social opportunity costs, causing individuals to

108   sacrifice sleep in order to spend more time actively engaging with group-mates. Additionally,

109   proximity to group-mates may cause cascading disruptions initiated by short periods of wakeful

110   activity of neighboring individuals. Thus, sleeping in close proximity to conspecifics may potentially

111   be accompanied by both costs and benefits for an individual's ability to obtain sufficient sleep, and

112   discovering how these potential costs and benefits are actually realized will shed light on the forces

113   that have guided sleep adaptations in social animals.

114   To understand how group-living animals navigate tradeoffs between their physiological need

115   for sleep and the ecological and social pressures that shape the costs and benefits associated with this

116   biological imperative, we investigated the factors shaping sleep patterns of wild olive baboons (*Papio*

117   *anubis*). Baboons live in stable multi-male, multi-female groups of up to 100 individuals (Cheney &

118   Seyfarth, 2008), and during the night, they seek safety in trees and rock outcroppings (Altmann &

119   Altmann, 1970; Busse, 1980). Despite seeking refuge in these sleep sites, baboons remain particularly

120   vulnerable to nighttime predation from leopards, which represents the single largest source of

121   mortality for adult baboons (Cheney et al., 2004; Cowlishaw, 1994; Isbell et al., 2018). Baboons must

122   therefore navigate the tradeoff between investing in sleep and maintaining anti-predator vigilance. As

123   a highly gregarious animal whose fitness depends heavily on their social relationships (Silk et al.,

124   2009), baboons must also balance their time spent sleeping with their investment in social

125   interactions, as time constraints during the day limit their ability to build and maintain their

126   relationships (Dunbar, 1992).

127   We simultaneously tracked the activity of 26 wild olive baboons from the same group using

128   collars fitted with GPS sensors and tri-axial accelerometers to understand how baboons manage their

129   competing nighttime priorities. Accelerometer-based sleep classification has shown an impressive

130   ability to detect and monitor sleep behavior across taxa (Ancoli-Israel et al., 2003; de Souza et al.,

131   2003; Hoffmann et al., 2012; Ladha & Hoffman, 2018; Malungo et al., 2021; Qin et al., 2020), and is

132   now commonly used to assess sleep in both humans (e.g. Jones et al., 2019; Patel et al., 2017) and

133   non-human animals (e.g. Gravett et al., 2017; Reinhardt, 2020; Samson et al., 2018). Validation

134   studies comparing performance of this non-invasive method to polysomnogaphy—the gold standard

135   in sleep research—generally show high accuracy (78-90%; Ancoli-Israel et al., 2003; Kanady et al.,

136   2011; Malungo et al., 2021; Shambroom et al., 2012), although concerns remain about the ability of

137   movement-based methods to distinguish sleep from resting wakefulness (Ancoli-Israel et al., 2003; de

138   Souza et al., 2003), and results must be evaluated with these caveats in mind. For this study, we

139   adapted a well-validated sleep classification algorithm used in human research (van Hees et al., 2015;

140   van Hees et al., 2018) and validated its ability to detect sleep in wild baboons. We then used this

141   algorithm to describe the sleep patterns of members of our study group over a period of a month

142   (Table S1). We used these data to assess the influence of homeostatic regulation on the pattern of

143   sleep and wake bouts within nights, as well as the duration of sleep across nights. We compared this

144   influence to that of the location in which individuals slept (both within the sleep site as well as

145   between distinct sleep sites) and their local social environment, both of which may exert pressures on

146   sleep behavior in the wild that conflict with the maintenance of homeostasis.

147   **Results**

148   The diel pattern of activity in wild baboons, as reflected by accelerometry data, reveals a clear

149   monophasic sleep pattern, with individuals active during the day and inactive at night (Fig. 1B). To

150   derive metrics of sleep (sleep onset time, awakening time, total sleep time, sleep period duration,

151   sleep efficiency), we calculated the log of the vectorial dynamic body acceleration (VeDBA), a

152   widely-used measure of overall movement activity (Qasem et al., 2012), from 36 calendar days or 354

153   baboon-nights. Sleep onset occurred 53.0 ± 1.7 (mean $\pm$ SE) minutes prior to the end of evening

154   astronomical twilight, and baboons awoke 35.9 ± 1.7 minutes after the beginning of morning

155   astronomical twilight (Fig. 1A,C). The duration of the sleep period – the period between sleep onset

156   and awakening – was 11.0 ± 0.04 hours on average. Within the sleep period, baboons slept for an

157   average of 9.2 ± 0.04 hours (total sleep time), displaying an average sleep efficiency of $85.0\% \pm$

158   0.2%.

159   [Figure 1]

160   Due to high correlation of total sleep time with onset time, awakening time, sleep period

161   duration, and sleep efficiency (Table S2), we focused the majority of our analyses on total sleep time.

162   Individuals differed in their total sleep time, and much of this variation reflected differences between

163   the sexes and variation across age categories. Males slept an average of 20 minutes longer than

164   females (Linear Mixed Model (LMM): standardized estimate [95% credible interval lower bound,

165   95% credible interval upper bound]: 0.44 [-0.04, 0.92]), while juveniles and subadults slept, on

166   average, 15 minutes less than adults (LMM: juveniles: -0.32 [-1.12, 0.50]; subadults: -0.32 [-0.80,

167   0.14]).

168   The maintenance of homeostasis was not a strong driver of sleep patterns (Fig. 2). After

169   sleeping poorly (low total sleep time), baboons did not 'catch up' by napping more on the following

170   day (Table S6; LMM: 0.05 [-0.08, 0.18]) or sleeping longer the following night (Fig. 2A; LMM: 0.00

171   [-0.14, 0.13]). However, baboons did sleep less following days on which they spent more time

172   napping (Fig. 2B; LMM: -0.18 [-0.36, -0.01]). For every minute spent napping, baboons spent 0.6

173   fewer minutes sleeping the following night. Baboons' sleep duration was uninfluenced by their

174   physical exertion during the day, as measured by either the distance they traveled (Fig. 2C; LMM: -

175   0.02 [-0.18, 0.15],) or their cumulative daytime VeDBA (Table S5; LMM: -0.12 [-0.33, 0.12]). In

176   humans, homeostatic regulation of sleep manifests within, as well as between nights: sleep wanes and

177   wakeful activity increases over the course of the sleep period as individuals gradually fulfill their

178   sleep requirements (Winnebeck et al, 2018). Baboons, in contrast, did not experience this increase in

179   wakefulness as the night progressed, despite exhibiting cyclic sleep patterns that are otherwise similar

180   to patterns of human sleep (Fig. 2D; GAMM: r^2_{adj} = 0.008, $F_{(8.741)}$ = 89.16, p < 1×10^{-15}).

181   [Figure 2]

182   The location where baboons slept had a strong influence on sleep duration, with individuals

183   sleeping less when spending the night in less familiar locations. For the first 21 nights of the study,

184   group members slept at the same site, distributed across ten adjacent yellow fever (*Acacia*

185   *xanthophloea*) trees (Fig. 3A). Individuals showed high fidelity to particular sleep trees (Fig. S3; one-

186   tailed two-sample Kolmogorov-Smirnov test: p < 1.0×10^{-9}), returning each night to one or a small set

187   of the available trees populated by the group. Not only did the choice of tree itself influence sleep

188   duration (Table S3 – S4, Fig. S4), but the individual's familiarity with their selected tree impacted

189   how much they slept. Baboons slept longer in trees to which they showed higher fidelity (Fig. 3C;

190   LMM: 0.20 [0.05, 0.36]), with individuals sleeping up to 33.3 minutes longer in the tree to which they

191   showed highest fidelity than in the tree to which they showed lowest fidelity. Following a failed

192   leopard attack on the 21st night of the study, the group moved to a less commonly used sleep site 1.5

193   km away (Fig. 3B). They remained at this sleep site for three nights before returning to sleep at their

194   main sleep site. While the baboons showed no substantial decrease in their sleep duration on the night

195   of the leopard attack (Fig. 3D, Fig. S7; LMM: -0.25 [-0.87, 0.39]), they slept 72 minutes less, on

196   average, upon moving to the less familiar sleep site (Fig. 3D, Fig. S7; LMM: -1.55 [-2.18, -0.91]).

197   This decrease in total sleep time following the change in sites was limited to the first night in the new

198   sleep site, after which sleep durations returned to normal (Fig. 3D; Fig. S7).

199   [Figure 3]

200   Sleeping in a social context also impacted sleep duration, as group-mates disrupted each

201   other's rest during the night. Contrary to predictions of the sentinel hypothesis, the proportion of the

202   night in which at least one individual was awake was significantly less than expected by chance (Fig.

203   4A; Fisher's exact test: p < 0.0001), suggesting that, rather than staggering periods of nocturnal

204   wakefulness, group-mates were actually synchronized in their sleep-wake patterns throughout the

205   night. Confirming this synchronization, we found that a significantly greater proportion of the group

206   exhibited the same simultaneous behavior, either being asleep or awake, than expected (Fig. 4B;

207   Fisher's exact test: p < 0.0001). Group members showed a unique pattern of synchronized sleep and

208   wake bouts each night, and thus, synchronization was not a spurious result of a stereotyped schedule

209   of activity that happened to be consistent across baboons and across nights (Fig. S10; Fisher's exact

210   test: p < 0.0001). Moreover, pairs of baboons showed more synchronization when sleeping in the

211   same tree than when sleeping in different trees (Fig. 4C; LMM: 0.56 [0.47 – 0.64]), which suggested

212   that sleeping individuals may awaken in response to the activity of group-mates in their local

213   environment, or that external disruptions in the local environment may simultaneously waken all

214   group members in the vicinity. To distinguish between these potential explanations, we tested the

215   influence of the number of group-mates in an individual's local environment on their total sleep time,

216   and found that individuals slept less when sharing their sleeping tree with more group-mates (Fig. 4D;

217   LMM: -0.51 [-0.85, -0.16]). Each additional tracked group-mate in a tree resulted in a 4.0-minute

218   decrease in total sleep time. Taken together, these results indicate that synchronization resulted from

219   social disruptions of sleep.

220   [Figure 4]

221   We found no influence of moon phase or the minimum ambient temperature during the night

222   on baboon sleep duration (LMM: Moon phase: 0.05 [-0.12, 0.22]; Temperature: -0.03 [-0.21, 0.13]).

223   **Discussion**

224   In this study, we demonstrate that the ecological and social demands that animals experience

225   in the natural world disrupt the widely-reported homeostatic regulation of sleep. We show that while

226   baboons sleep less in unfamiliar environments and their sleep is disrupted by the activity of group-

227   mates, their recent history of sleep and physical exertion has only a limited role in influencing sleep

228   behavior. Because baboons are highly vulnerable to nocturnal predation (Busse, 1980; Cheney et al.,

229   2004; Isbell et al., 2018) and because they experience fitness benefits from maintaining strong social

230   bonds (Silk et al., 2009), sacrificing sleep to maintain alertness in novel environments and to remain

231   close to group-mates may represent critical adaptations. Our results highlight the tradeoffs that group-

232   living animals navigate when investing in sleep in the wild, and in doing so, challenge the centrality

233   of the role that homeostasis has played in shaping sleep patterns in the environment in which sleep

234   evolved. Decades of research in the laboratory and at the bedside have implicated homeostatic

235   regulation as a key driver of sleep patterns, with the sleep rebound that follows periods of deficit

236   facilitating the maintenance of a physiologically required amount of sleep (Amlaner et al., 2009).

237   However, sleep studies have traditionally investigated sleep in highly controlled environments, where

238   the costs of investing in sleep are largely absent. Our findings suggest that, in the natural world,

239   "sleep need" may be a relatively flexible concept, with variation in sleep investment driven as much

240   by the opportunity costs of sleep as by its physiological benefits.

241   There are substantial opportunity costs of devoting a significant portion of every day to

242   sleeping. Sleeping animals are highly vulnerable to predation (Lima et al., 2005), and our results

243   suggest that individuals sleep less when the risk of predation is particularly high. Baboon group

244   members showed high fidelity to particular locations within their main sleep site, and individuals

245   sacrificed sleep both when sleeping in trees to which they did not show high fidelity as well as upon

246   moving to a new, less familiar sleep site following a leopard attack. Given that predation risk tends to

247   be greater in unfamiliar locations (Forrester et al., 2015; Gehr et al., 2020; Yoder et al., 2004),

248   baboons appear to trade sleep for vigilance according to the current risk of predation. Notably,

249   however, we did not find that baboons decreased their investment in sleep on the night of leopard

250   attack. This surprising result may reflect leopards' disinclination, as stealth hunters, to launch

251   repeated attacks (Hayward et al., 2006; Lin et al., 2020), or indicate that baboons perceive uncertainty

252   in the level of risk as potentially more dangerous than a confirmed threat.

253   Engaging in sleep precludes investment in a variety of behaviors, in addition to anti-predator

254   vigilance, that are important to fitness (Aulsebrook et al., 2016; Lesku et al., 2012; Lima et al., 2005;

255   Roth et al., 2010). Consistent with our results, recent studies in ecologically-relevant contexts have

256   revealed that animals forego sleep when ecological demands increase the associated opportunity costs.

257   For example, while engaging in long, non-stop flights, great frigatebirds reduced the amount they

258   slept by 92.7%, without apparent physiological consequences (Rattenborg et al., 2016). Similarly,

259   northern fur seals (*Callorhinus ursinus*) experience extended suppression of rapid eye movement

260   (REM) sleep – also shown in the laboratory to be homeostatically regulated (Dement, 1960;

261   Shiromani et al., 2000) – when they migrate in the open ocean for several months (Lyamin et al.,

262   2018). Moreover, the seals do not experience a rebound in their REM sleep following this period of

263   deficit (Lyamin et al., 2018). Male pectoral sandpipers greatly reduce their time spent sleeping during

264   their short and intense mating season, and males that slept less actually experienced higher

265   reproductive success (Lesku et al., 2012). Thus, across contexts and taxa, ecological pressures appear

266   to supersede the maintenance of sleep homeostasis in the wild.

267   Recent technological advances allowing for the use of polysomnography – the gold standard

268   for recording sleep – have played an important role in revealing the ecological tradeoffs that wild

269   animals face when navigating decisions about when, where, and how to sleep (Davimes et al., 2018;

270   Lesku et al., 2011, 2012; Rattenborg et al., 2008, 2016; Scriba et al., 2013; Voirin et al., 2014).

271   Although these advances hold great promise for wider application in the future, the invasive nature of

272   polysomnography unfortunately limits its current use to taxa whose daily activities do not interfere

273   with electrodes implanted either subdermally or inter-cranially. Because baboons are highly dexterous

274   and engage in frequent allogrooming, we were unable to apply this gold standard, and instead,

275   resorted to an alternate method in order to ask and answer important questions about the ecology of

276 sleep in a wild social primate. Accelerometer-based sleep classification – a tool already used to

277 investigate sleep across terrestrial (human: Jones et al., 2019; Patel et al., 2017; non-human: Bäckman

278 et al., 2017; Davimes et al., 2018; Gravett et al., 2017; Lesku et al., 2011; Malungo et al., 2021; Qin et

279 al., 2020; Reinhardt et al., 2019; Reyes et al., 2021; Samson et al., 2018; Sellers & Crompton, 2004;

280 Sri Kantha & Suzuki, 2006; Suzuki et al., 2018) and marine taxa (Miller et al., 2008; Mitani et al.,

281 2010; Wright et al., 2017) – offered a valid alternative to polysomnography. We note that the use of

282 accelerometry can introduce biases in sleep monitoring, typically by overestimating total sleep time as

283 a result of an inability to distinguish resting wakefulness from sleep (Ancoli-Israel et al., 2003; de

284 Souza et al., 2003). However, if these biases are considered during the interpretation of results, the use

285 of accelerometry to investigate sleep provides an immediate opportunity to shed light on how diverse

286 species balance their physiological sleep requirements with ecological opportunity costs that vary

287 according to natural history, trophic level, community composition, climate, and local environment.

288 Further, the relative ease of accelerometer deployment, and its prevalence in ecological research,

289 changes the scale at which sleep behavior can be studied, enabling the simultaneous and long-term

290 monitoring of sleep at the population level. This rescaling of sleep research creates many new

291 opportunities, one of which is the ability to record sleep in the majority of social group members and

292 thus explore an exciting new scientific frontier: the collective dynamics of sleep.

293   Using accelerometry to track the sleep patterns of nearly an entire group of wild baboons, we

294 demonstrated the importance of the social environment in shaping the sleep patterns of group-living

295 animals. Contrary to the predictions of the sentinel hypothesis (Samson et al., 2017; Snyder, 1966),

296 periods of nocturnal wakefulness of group members were not staggered, but rather synchronized,

297 particularly with nearby group-mates. Baboons also slept less when in close proximity to a greater

298 number of group-mates. Taken together, these results suggest that group-mates disrupt each other's

299 sleep. Social disruptions may result from group-mates actively interacting with each other during the

300 night. Gregarious animals often invest substantially in building and maintaining social relationships

301 with their group-mates (Ward & Webster, 2016), and these bonds can prove essential to their fitness

302 (Cameron et al., 2009; Campos et al., 2020; Frère et al., 2010; Riehl & Strong, 2018; Silk et al.,

303 2009). Because animals have limited time to devote to maintaining their social bonds during the day

304 (Dunbar, 1992), they may actively sacrifice sleep in order to invest in these relationships at night.

305 Alternatively, social animals may wake in response to the periodic waking and repositioning of their

306 group-mates during the night, and thus, socially-disrupted sleep may be an inherent by-product of

307 sleeping in a group. Simply remaining in a cohesive group may therefore present a challenge to

308 obtaining sufficient sleep.

309   Social animals may jeopardize sleep homeostasis to maintain cohesion with their conspecifics

310 because remaining in close proximity to their group-mates during the sleep period could prove

311 essential to their fitness. Individuals likely benefit from the dilution of predation risk that is achieved

312 through group cohesion, particularly when they are sleeping and thus highly vulnerable to predators

8

313   (Lehtonen & Jaatinen, 2016). Collective vigilance may also reduce the risk of predation for group

314   members. Even in the absence of collective vigilance optimization via non-randomly staggered

315   wakefulness, the proportion of the night with at least one group member awake is still likely to be

316   substantially greater than any particular individual's investment in vigilance. In our study, at least one

317   individual in the group was awake for 394 ± 11 minutes ($82\% \pm 2\%$) from 21:00 to 05:00, although

318   each individual was only awake for 79 ± 1 minutes ($16\% \pm 0.2\%$) of the same period. Samson and

319   colleagues (2017) found high levels of collective vigilance during the night in a group of Hadza

320   hunter-gatherers, and they suggest that this collective vigilance may facilitate higher intensity sleep

321   (Samson & Nunn, 2015). Because accelerometry cannot measure sleep intensity, we were unable to

322   test whether collective vigilance allowed individuals sleeping close to group-mates to experience

323   more intense, albeit shorter, sleep. Future studies leveraging advances in polysomnography (i.e. EEG)

324   that may eventually allow its application in wild social animals could enable a test of this possibility.

325   Unexpectedly, we found that adult baboons slept longer than subadults and juveniles, and

326   males slept longer than females. This contrasts with previous research that found age differences in

327   sleep patterns linked to physiological demands during the development of the central nervous system

328   (Amlaner et al., 2009) and sex differences in sleep tied to the influence of sex steroids (Mong &

329   Cusmano, 2016), with younger individuals sleeping more than older individuals (Knutson, 2014;

330   Ohayon et al., 2004; Olds et al., 2010; Steinmeyer et al., 2010; Stuber et al., 2015) and females

331   sleeping more than males in birds and humans (Lendrem, 1983; Mong & Cusmano, 2016; Roehrs et

332   al., 2006; Steinmeyer et al., 2010; Stuber et al., 2015). Our surprising results here may be an artefact

333   of the tendency of accelerometer-based sleep monitoring to classify resting wakefulness as sleep

334   (Table S12; Ancoli-Israel et al., 2003; de Souza et al., 2003). Older individuals may rest quietly when

335   waking during the night, thus falsely determined to be asleep according to their accelerometry,

336   whereas younger individuals may be more likely to resume activity upon waking. However, if these

337   findings are not the result of a bias in our sleep recording technique, they may reflect variation in the

338   vulnerability to predation among the age-sex classes in this highly sexually dimorphic species

339   (Cheney et al., 2004), with young and female baboons likely realizing a higher cost of sleep than adult

340   males. Individuals may also differ in their sleep patterns due to their ability to gain access to a high-

341   quality sleep location within the group's sleep site. Our results have demonstrated the importance of

342   location to sleep duration. However, group-mates may differ in their access to preferred sleep

343   locations, particularly if preferred locations are limited. Baboon groups are structured by linear

344   dominance hierarchies that shape the priority of access to resources (Cheney & Seyfarth, 2008; King

345   et al., 2009; Marshall et al., 2015), and individuals can leverage their affiliative and kinship

346   relationships to obtain resources that they would not be able to access based on social rank alone (Sick

347   et al., 2014). Further research is needed to investigate the extent to which these complex social

348   dynamics influence an individual's ability to obtain a preferred sleep location and, thus, a good

349   night's sleep.

9

350   In addition to highlighting social dynamics as a key driver of sleep patterns in group-living

351   species, our study provides important insights into selective pressures that may have shaped the

352   evolution of human sleep. The physiological requirements for sleep and the homeostatic mechanisms

353   that ensure this requirement is fulfilled have long been assumed to be the key drivers influencing the

354   way that our sleep has evolved and the characteristics of our sleep today. However, we suggest that

355   the criticality of homeostatic control in shaping our sleep patterns could be an artefact of sleeping in

356   an environment devoid of the ecological and social costs that sleep would have presented our

357   ancestors. Evidence suggests that, like baboons, early hominins were extremely vulnerable to

358   nighttime predation in their dry savannah habitats (Brain, 1983; Treves & Palmqvist, 2007;

359   Wrangham & Carmody, 2010). Hominins likely remained vulnerable to nocturnal predation until they

360   began to manipulate fire, around which they could sleep to reduce the risk of predation (Samson &

361   Nunn, 2015), and some characteristics of our sleep today may be best explained in light of the

362   vulnerability that sleep imparted on our ancestors. For example, modern humans exhibit decreased

363   sleep quality when sleeping in an unfamiliar environment (Tamaki et al., 2016), similar to the

364   baboons in our study. The lower quality sleep resulting from this aptly named "first night effect" is

365   limited to the first night in a new location (Tamaki et al., 2016), and our findings suggest that the first

366   night effect may be conserved from an environment where this first night would have been

367   accompanied by poor information about risk and thus, a higher likelihood of predation. Early

368   hominins would have also experienced a social opportunity cost of sleep, as they likely slept in groups

369   (Samson & Nunn, 2015; Willems & van Schaik, 2017) and would have experienced constraints on the

370   time available to maintain their social network during the day, until developing the advanced

371   cognition that enabled a more efficient use of time (Nunn & Samson, 2018; Samson & Nunn, 2015).

372   While our sleep has likely evolved substantially from that of our earliest ancestors, with modern

373   human sleep being extremely short and intense compared to that of other primates (Nunn et al., 2016;

374   Nunn & Samson, 2018), a full understanding of the way we sleep involves considering not only the

375   physiological benefits of sleep, but also its ecological and social costs in the environment in which it

376   evolved.

377   **Materials and Methods**

378   *Data collection*

379   We monitored sleep and activity patterns in a group of olive baboons at Mpala Research

380   Centre (MRC), a 200 km^2 conservancy located on the Laikipia Plateau in central Kenya. We trapped

381   and anesthetized 26 individuals, which comprised more than 80% of the adults and subadults in the

382   study group (see Strandburg-Peshkin et al., 2015 for details on capture methodology). Upon capture,

383   we noted the age class and sex of each baboon, as well as whether the baboon was lactating. We fit

384   each individual with a GPS and accelerometry collar that recorded the baboon's GPS location at 1 Hz

385   sampling interval and continuous tri-axial accelerations at 12 Hz/axis from 06:00 to18:00. From 18:00

386   to 06:00, the collars recorded a 2.5-second burst of accelerations at 10 Hz/axis at the beginning of

387 every minute. The collars were programmed to collect data from August 1, 2012 to September 6,

388 2012, but due to a programming glitch, several collars stopped collecting data prematurely (Table S1).

389 In total, we collected 483 days of GPS data, and 506 nights of accelerometry data. We also collected

390 high-resolution drone imagery of the group's most commonly used sleep site (see Strandburg-Peshkin

391 et al., 2017 for details).

392 *Sleep Analysis*

393 We used the accelerometry data to classify sleep behavior by adapting a method presented in

394 van Hees et al. 2018 that was developed for extracting metrics of sleep in humans from wearable

395 accelerometry devices. The process of determining the sleep period, defined as the period from sleep

396 onset to waking, is summarized in Fig. 5.

397 To uniformize the accelerometry sampling schedule, we down-sampled and interpolated the

398 daytime accelerometry data such that it matched the 10 Hz bursts of accelerometry collected during

399 the night. We calculated the vectorial dynamic body acceleration (VeDBA) using a 0.7-second time-

400 window and generated the log of the average VeDBA for the 2.5-second burst each minute. We then

401 calculated a rolling median of the log VeDBA with a 9-minute window. Following van Hees et al.

402 2018, continuous periods of at least 30 minutes during which the rolling median of the log VeDBA

403 was less than the 10th percentile of the log VeDBA multiplied by 1.125 were considered sleep blocks.

404 Any blocks within 45 minutes of each other were merged into sleep periods. If this resulted in more

405 than one sleep period, the longest sleep period in the day, defined as a noon-to-noon period, was

406 considered the sleep period. The beginning and end of the sleep period represents the time of sleep

407 onset and waking, respectively. Of the 506 baboon-nights of accelerometry data, we successfully

408 calculated the sleep period for 491 baboon-nights.

409

410 [Figure 5]

411 Adapting the method developed by van Hees and colleagues (2015), we classified each

412 minute epoch both within and outside of the sleep period as representing either sleep or waking

413 behavior. As above, the 10th percentile of the log VeDBA multiplied by 1.125 served as the

414 classification threshold, and we classified epochs as indicating sleep when the log VeDBA for at least

415 three consecutive epochs was below the log VeDBA threshold value. We classified all other epochs as

416 representing waking behavior. Consistent with previous sleep analyses, we measured total sleep time

417 as the total number of minutes of sleep epochs during the sleep period. We measured sleep efficiency

418 as the total sleep time divided by the duration of the sleep period. We measured sleep time during the

419 day – time spent napping – as the number of minutes of sleep epochs from 07:30 to 17:30, as these

420 times were reliably within the waking period (Fig. 1C), and using standardized times prevented a

421 spurious negative correlation between time spent sleeping during the waking period and total sleep

422 time during the sleep period that would result from the waking period prior to or following short sleep

423 periods having a greater number of potential epochs that could be considered sleep.

11

424   The accelerometer units occasionally failed to collect data according to their programmed
425   sampling schedule. Because insufficient data in a given day would prevent a reliable calculation of the
426   threshold value for the sleep classification and produce variability in the number of potential sleep
427   epochs, we did not include data for total sleep time, sleep onset time, waking time, or napping time
428   (both on the prior day and following day) from noon-to-noon periods missing at least 120 (8.3%)
429   accelerometry bursts, which decreased the number of baboon-nights from 491 to 368. We further
430   removed data for total sleep time, onset time, and waking time from noon-to-noon periods missing at
431   least 20 consecutive accelerometry bursts, as the determination of the sleep period is sensitive to gaps
432   between consecutive accelerometry bursts, resulting in a final number of 354 sleep periods analyzed.
433   We did not remove data for napping time on these days because measuring napping time did not
434   depend on the determination of the sleep period.

435   *Validation of sleep classification algorithm*

436   The algorithm from which the sleep classification technique is adapted is well-validated using
437   polysomnography (C-statistic = 0.83 – 0.86) to both classify sleep behavior and determine the sleep
438   period in humans (van Hees et al., 2015, 2018). Although the classification of sleep in non-human
439   primates using devices and algorithms that were validated with polysomnography only in humans has
440   become a common practice in sleep research (Barrett et al., 2009; Brutcher & Nader, 2013; Reinhardt
441   et al., 2019; Reyes et al., 2021; Samson et al., 2018; Sri Kantha & Suzuki, 2006; Zhdanova et al.,
442   2002), we returned to the study site in July 2019 to validate the accelerometer-based sleep
443   classification. Because logistical and ethical limitations prevent the use of polysomnography in free-
444   ranging, highly dexterous animals, we compared the accelerometer-based sleep classification to direct
445   observations of wakeful and sleeping baboons fit with accelerometer collars for validation, as
446   suggested by Rattenborg and colleagues (2017). Behavioral observations were facilitated by high-
447   resolution thermal imagery (FLIR T1020, FLIR Systems Inc., Wilsonville, OR, USA). The validation
448   study determined that our accelerometry-based classification of sleep exhibits a 79.9% accuracy
449   (Table S12; see Supplemental Information for further details of validation study).

450   *Physical activity*

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

460   We also calculated cumulative activity during the day from the accelerometry data. Using the

461   continuous 12 Hz accelerometry data, we calculated VeDBA from 06:00 to 18:00 using a 0.5 second

462   time window, averaged VeDBA over each minute, and then summed these values to generate a

463   cumulative measure of activity during the day.

464   *Sleep location characterization and fidelity*

465   Visualization of the GPS data indicated that individuals remained reliably stationary until at

466   least 06:15 every day, and thus we determined the location in which each baboon slept from the

467   median of the first 10 GPS locations that occurred before 06:15. If an individual's GPS collar did not

468   successfully collect 10 locations before 06:15, its data on this day were excluded from analyses

469   involving sleep location. This resulted in the removal of 9/483 baboon-days of data. In ArcGIS, drone

470   imagery was used to trace the crowns of distinct sleep trees within the group's main sleep site. We

471   determined that an individual slept in a particular tree if its sleep location was within the traced

472   polygon of that tree crown. Sleep locations that fell outside the crown of a tree, likely reflecting minor

473   error in the GPS location estimates, were assigned to the closest sleeping tree. Only 32/469 sleep

474   locations (6.8%) had to be assigned to a sleep tree in this manner. In rare cases where an individual's

475   sleep location was greater than 10 m from the crown of the closest sleep tree (5/474 cases – 1.1% of

476   baboon-days), its data on this day were excluded from analysis.

477   Analysis of the sleep location data revealed that, over the course of the study, the baboons

478   slept in two distinct sleep sites that were separated by approximately 1.5 km. The group slept at their

479   main sleep site for the first 21 nights of the study, and then spent three nights in a different sleep site

480   after a failed leopard attack on the 21st study night. The group then returned to the main site for the

481   duration of the study. In total, they spent 32/35 (91.4%) nights at their main site and 3/35 (8.6%)

482   nights at the alternate sleep site. While the entire group slept in a single tree at the less frequently used

483   sleep site, the group's main sleep site contained 10 trees across which the group slept. We performed

484   a permutation test to investigate whether individuals exhibited consistency in the tree in which they

485   chose to sleep. We calculated the Shannon entropy of each individual's sleep tree usage, and we

486   compared these Shannon entropies to those produced from each of 1000 random exchanges of the

487   locations of individuals on each night. Permuted values provide a null distribution controlling for

488   potential sleep tree usage, as the distribution of individuals across the sleep trees each night from the

489   empirical data was maintained in the permuted data. Shannon entropy is a measure of the uncertainty

490   of a random variable, and is given by the equation:

491
$$H(X) = -\sum_{X=x} p(x)log\big(p(x)\big)$$

492   Thus, a lower Shannon entropy in the empirical data compared to the permuted data in this context

493   would signal sleep tree fidelity, with an individual sleeping more often in certain trees and less often

494   in other trees than expected by chance. To determine whether the baboons exhibited significant sleep

495   tree fidelity, we compared the distribution of the group's empirical entropies to the distribution of

496   entropies produced from the permutations with a one-tailed two-sample Kolmogorov-Smirnov test.

497   As determining fidelity requires several nights of data, we did not include entropy values, either

498   empirical or permuted, from individuals with less than four nights of data. We also limited this

499   analysis of tree fidelity to the first 15 days of data, as the number of individuals on which we have

500   data decreases sharply after this day (Table S1), which decreases the possible permutations.

501   After determining that individuals showed non-random sleep tree selection (see Results), we

502   then calculated an individual-specific fidelity index for each tree. This fidelity index was measured as

503   the average number of nights an individual slept in a particular tree in the 1000 permutations

504   subtracted from the number of nights the individual actually slept in that particular tree. Again, we did

505   not calculate fidelity indices for individuals with less than four nights of data.

506   *Pattern of sleep-wake behavior across the group*

507   We tested whether individuals staggered their periods of nocturnal wakefulness or,

508   conversely, synchronized them beyond the level expected by chance. For this analysis, we subset the

509   data to times between 21:00 and 05:00, as these times consistently fell within the bounds of the sleep

510   period of all individuals. We calculated the proportion of minute epochs across all nights in which at

511   least one group member was awake and the proportion of the group that was synchronized in their

512   behavior (either sleep or wakefulness) during each minute epoch, averaging across all epochs. We

513   then calculated these same proportions, but after applying a random time shift to each individual's

514   time series of sleep-wake epochs on each night (Fig. S9). We repeated this procedure 1000 times to

515   develop a null distribution of the proportion of epochs during the night in which at least one

516   individual is awake and a null distribution of the average proportion of the group that was

517   synchronized, and we compared the empirical proportions to their respective null distributions

518   statistically with a Fisher's exact test. The p-value thus represents the proportion of time-shifted

519   values that were as extreme or more extreme than the empirical value. Shifting the data in time rather

520   than permuting it allowed us to develop null distributions while maintaining the autocorrelation

521   structure of the data.

522   To confirm the robustness of our findings, we again tested for collective vigilance and

523   synchronization, comparing the empirical values defined above to null distributions produced using an

524   alternative method. In this method, rather than applying a random time shift to each night of each

525   individual's data, we maintained the real time associated with the time series data, but we permuted

526   the night associated with each time series (Fig. S10). We compared empirical values to the null

527   distributions created by these night permutations with a Fisher's exact test.

528   *Statistical analysis of sleep*

529   Data were processed using the statistical analysis software R version 4.0.5 (R Core Team,

530   2021). We only included the first 20 study nights in the analyses of sleep, except where specified, due

531   to concerns that the leopard attack that occurred on the 21st night could potentially disrupt typical

532   sleep patterns. To compare the effects of various physiological, ecological, and social predictors of

14

533   sleep, we modeled total sleep time with a Bayesian linear mixed model (LMM), with random effects
534   of individual identity and night, and fixed effects of age, sex, distance traveled in the preceding day,
535   napping time during the preceding day, relative time spent sleeping the previous night, the identity of
536   the sleep tree, fidelity index for the current sleep tree, the relative number of individuals in the sleep
537   tree, the phase of the moon, and minimum ambient temperature during the night. We created a
538   separate model that included cumulative VeDBA instead of distance travelled because cumulative
539   daytime VeDBA was highly correlated with distance travelled during the day. An individual's relative
540   time spent sleeping the previous night was measured as the difference between its total sleep time on
541   the previous night and its average total sleep time. This relative measure controlled for positive
542   correlations between total sleep time on previous night and current night total sleep time that would
543   result purely from among-individual variation in total sleep time – a scenario that would not be
544   sufficiently controlled for by the individual identity random effect in this model. We calculated the
545   relative number of individuals in the sleep tree by dividing the number of individuals in the sleep tree
546   by the total number of individuals who were successfully assigned to a sleep tree on that given night,
547   to control for the decrease in the number of individuals in each sleep tree over the course of the study
548   that resulted from premature termination of data collection in several collars. Moon phase was a
549   continuous variable realizing values from 0 to 1 (with 0 representing a new moon, and 1 representing
550   a full moon), and we collected this data for the days of the study using the sunCalc package in R
551   (Benoit & Elmarhraoui, 2019). The minimum ambient temperature represented the minimum
552   temperature at the sleep site during the night, determined using interpolated ECMWF air temperature
553   (2 m above ground) data obtained with the Env-DATA functionality (Dodge et al., 2013) provided on
554   Movebank data repository (www.movebank.org). We standardized all response and predictor
555   variables to allow for comparison of effect sizes among variables. To increase the interpretability of
556   the total sleep time model, we reran the model without standardized variables. Effect sizes reported in
557   the main text are derived from the standardized model, whereas figures produced in the main text, as
558   well as the interpretation of the effect of each variable on the unstandardized sleep time are derived
559   from the model with unstandardized variables.

560   To examine the effect of the leopard attack and subsequent sleep site change on sleep
561   parameters, we modeled the effect of particular nights on sleep parameters with a Bayesian LMM.
562   Specifically, we divided data into the following categories: all nights before the leopard attack, the
563   night of the leopard attack, the first night in the new sleep site (i.e. the night following the leopard
564   attack), the second night in the new sleep site, the third night in the new sleep site, and the remainder
565   of study nights, during which the group slept in its main sleep site. Aside from this categorical night
566   variable, we also included age, sex, distance traveled in the preceding day, napping time during the
567   preceding day, relative time spent sleeping the previous night, the phase of the moon, and minimum
568   ambient temperature as fixed effects in the models with random intercepts for individual identity. In

569 these models, we did not include sleep tree identity, number of individuals in the sleep tree, and sleep

570 tree fidelity score, as the entire group slept in a single tree in the less commonly used sleep site.

571   We further tested for the effect of prior sleep debt on sleep behavior by modeling the effect of

572 total sleep time on time spent napping the following day. We modeled this relationship with a

573 Bayesian LMM, using individual identity and day as random intercepts. We also assessed how the

574 likelihood of sleep progressed through the night. We used a generalized additive mixed model

575 (GAMM) to model the log-odds of a baboon being asleep in a given epoch as a function of the

576 duration of that epoch from the beginning of the sleep period, scaled such that 0 represents the

577 beginning of the sleep period and 1 represents the end of the sleep period. We included individual

578 identity and night as random intercepts, and to account for autocorrelation in the response variable, we

579 also included an AR1 term in the model.

580   Lastly, we tested whether individuals showed higher synchronization of their sleep-wake

581 patterns when sharing the same sleep tree than when inhabiting different trees. With a Bayesian

582 LMM, we modeled the synchronization score between dyads on each night, calculated as the number

583 of minutes from 21:00 to 05:00 in which members of the dyad exhibited the same behavior divided by

584 the total number minutes in which both individuals had data. We included a binary predictor variable

585 indicating whether dyad members were in the same tree as the only fixed effect variable, and night,

586 the identity of both individuals in the dyad, as well as the identity of the dyad as random intercept

587 variables.

588   We carried out all Bayesian analyses with the "brms" package in R (Bürkner, 2017). We used

589 diffuse, mean-zero Gaussian priors for all predictor variables. Model estimates are based off of four

590 independent Hamiltonian Monte Carlo chains with 5000 iterations, 2500 of which were burn-in

591 iterations. Trace plots indicated that mixing was sufficient and that the four chains converged on the

592 same posterior region. Model estimates reported in the text represent the mean of the posterior

593 distribution, along with the lower and upper 95% credible interval bounds from the standardized

594 models. We used package "mgcv" in R (Wood, 2011) to fit the GAMM to the sleep epoch data, using

595 a thin plate spline smoothing term with 10 knots.

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617 **Author Contributions**

618   J.C.L., R.H., and M.C.C. conceived the project. M.C.C. oversaw the data collection. J.C.L.,

619 R.H., and C.L.N analyzed the data and prepared the figures. J.C.L. led the writing of the manuscript,

620 to which all authors contributed.

621 **Competing interests**

622   The authors declare no competing interests.

623 **Data availability**

624   GPS and accelerometry data generated during this study are published and available in the

625 Movebank repository (www.movebank.org; Crofoot et al. 2021). Drone imagery is publicly available

626 for download from Dryad (http://dx.doi.org/10.5061/dryad.6h5b7). Accelerometry data and

627 behavioral scoring data from the 2019 sleep validation study is also publicly available for download

628 from Dryad (https://doi.org/10.5061/dryad.p5hqbzkqf).

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943 **Figures**
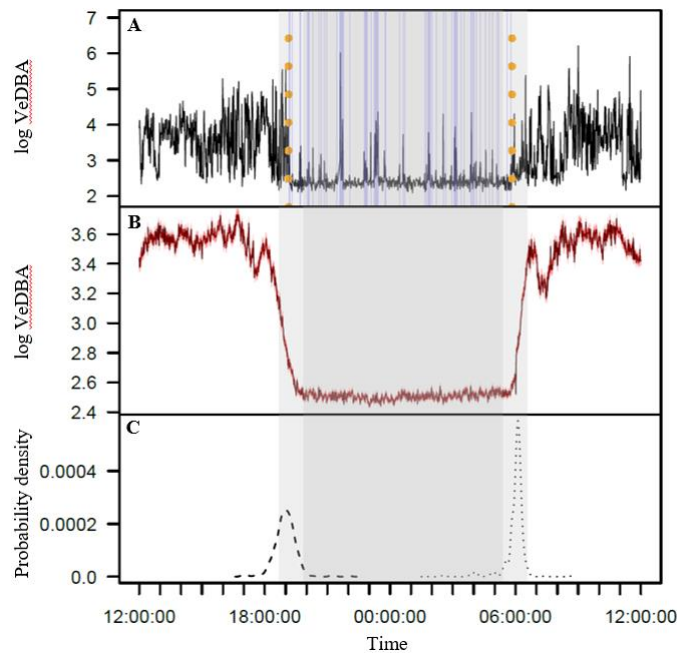
944

945 **Figure 1. Extracting activity and sleep from accelerometry in a group of wild olive baboons.** Adapting

946 algorithms developed by van Hees and colleagues (2015, 2018), we used the vectorial dynamic body

947 acceleration (VeDBA), a measure of overall activity, to determine the sleep onset and awakening times (A;

948 orange dotted lines), as well as periods of wake after sleep onset (A; blue shading) for each individual baboon

949 on each day. These metrics allowed us to calculate the total sleep time, sleep period duration, and sleep

950 efficiency as well. The plot (A) shows the data of one individual within a single noon-to-noon period as an

951 example. Averaged across all individuals on all nights (N = 354 baboons-nights), the log VeDBA shows that

952 baboons exhibit activity patterns typical of a diurnal animal with monophasic sleep (B), with a consolidated

953 period of very low levels of activity during the night. Although the timing of waking (C; dotted line) was more

954 consistent across the group and across the study period than the timing of sleep onset (C; dashed line), both

955 sleep onset and waking typically occurred within astronomical twilight. The red shading in (B) indicates ± 1 SE.

956 In all subplots, the grey shaded region depicts the period between sunset and sunrise, with double shading from

957 the end of astronomical twilight to the beginning of morning astronomical twilight.

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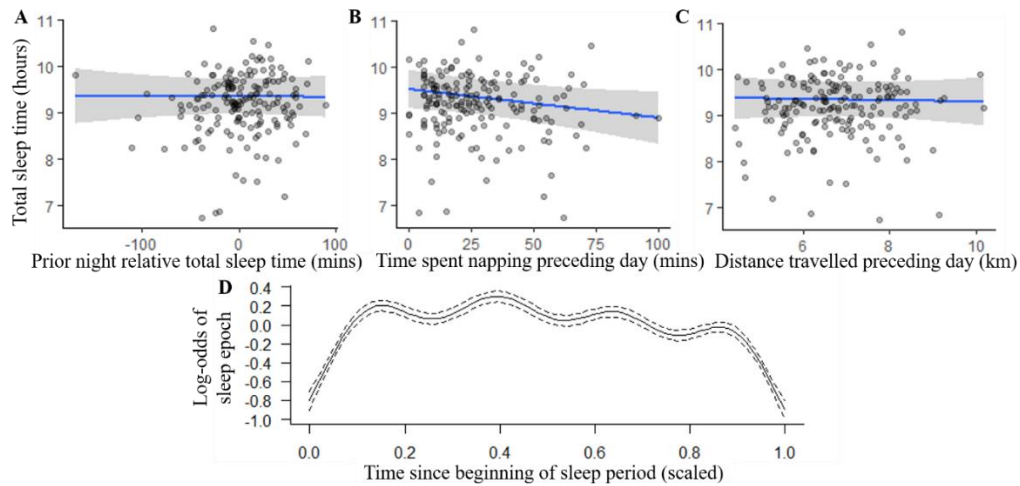
Figure 2. Homeostatic regulation has a weak influence on baboon sleep patterns. Neither the relative sleep time on the previous night (the difference between an individual's total sleep time and its average total sleep time; A) nor the distance travelled on the preceding day (C) influenced sleep duration, although baboons did sleep less following days with more napping (B). Additionally, the likelihood of a baboon being asleep did not substantially decrease as the night progressed and the baboon payed off its sleep debt (D). In (D), 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.

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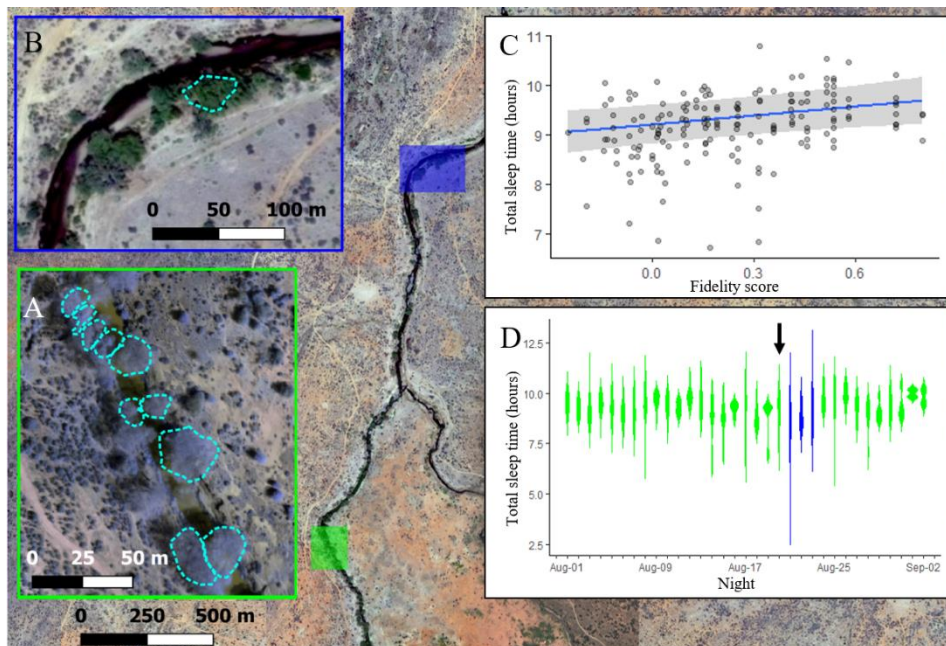
Figure 3. The location where baboons sleep has consequences on sleep duration. Group members spent the majority of the study (32/35 nights) sleeping in 10 yellow fever (*A. xanthophloea*) trees in a grove along the Ewaso Ng'iro river (A). Within this sleep site, baboons slept longer when sleeping in trees to which they showed high fidelity (C). At 20:30 on the 21st night of the study, a leopard mounted an unsuccessful attack on the group in their 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,

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977   with raw data points overlaid, and (D) depicts a violin plot of the data, with color corresponding to the sleep site

978   (A and B). The arrow in (D) indicates the night on which a leopard launched a failed attack on the group.

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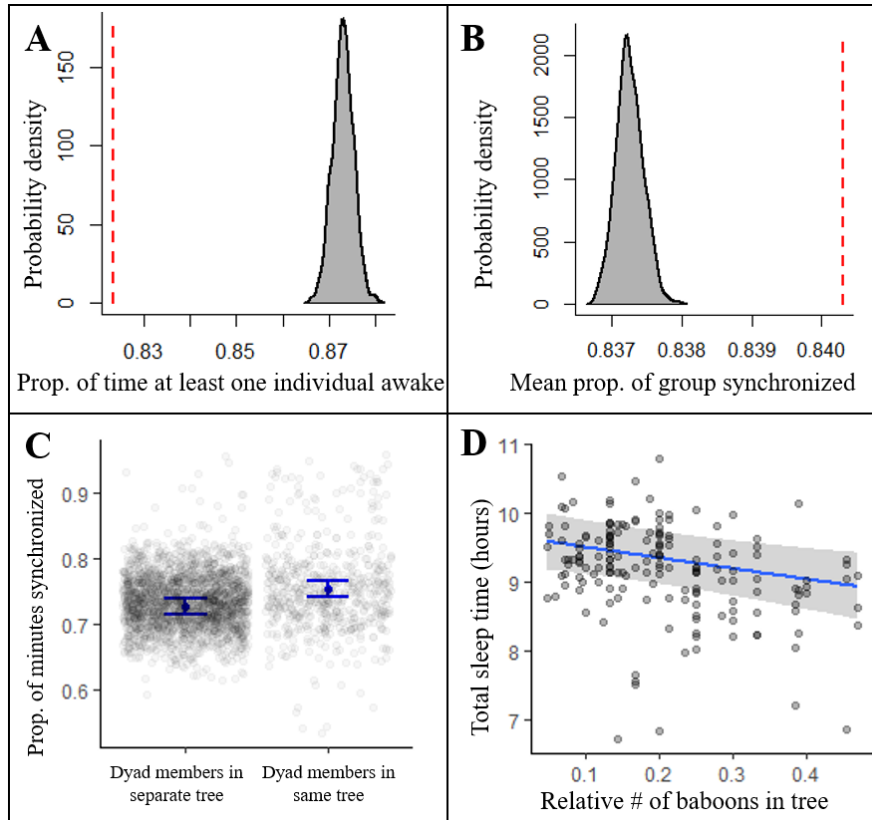
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982   **Figure 4. Collective dynamics within the sleep site influence sleep patterns.** Group-mates' periods of

983   nocturnal wakefulness were not staggered, but rather synchronized, as indicated by a significantly lower

984   proportion of time with at least one individual awake (A, dotted red line; Fisher's exact test: $p < 0.0001$) and a

985   significantly greater proportion of the group exhibiting synchronized behaviors (B, dotted red line; Fisher's

986   exact test: $p < 0.0001$) than expected based on 1000 time-shifted data sets (gray distribution). Synchronized

987   sleep patterns likely result from individuals waking in response to the nighttime activity of nearby group-mates,

988   as dyads show greater synchronization when dyad members sleep in the same tree compared to when they sleep

989   in different trees (C). As a consequence of these local social perturbations, baboons sleep less when sleeping in

990   trees with more group-mates (D). Subplots (C) and (D) depict the conditional effects from models of the data,

991   with raw data points overlaid.

*Day defined from noon to noon
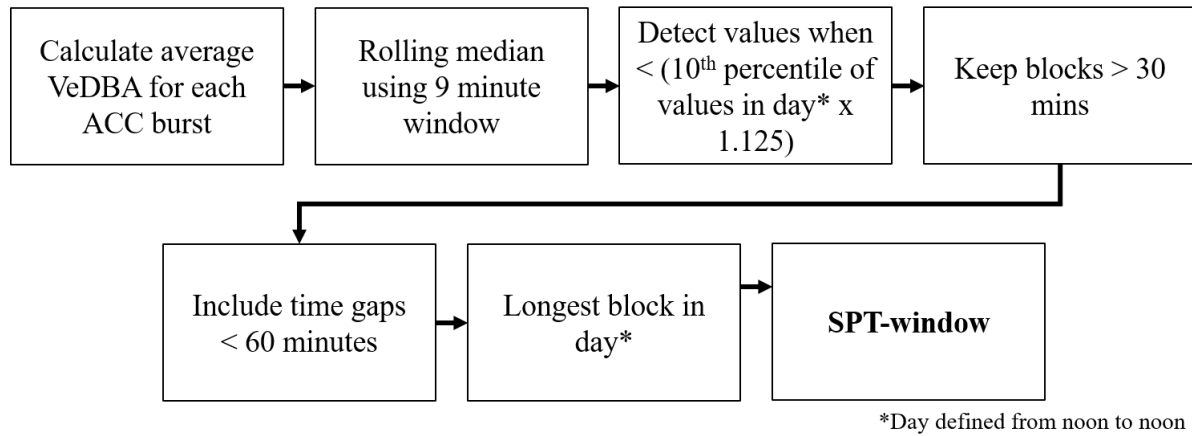
Figure 5. SPT-window detection algorithm adapted from van Hees et al., 2018.

Supplemental Information

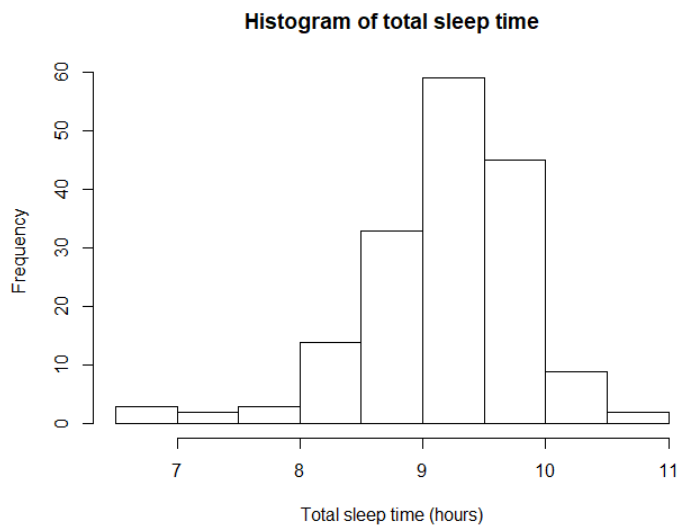| Collar #	GPS start date	GPS end date	ACC start date	ACC end date
2426	2012-08-01	2012-08-30	2012-08-01	2012-08-31
2427	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2428	2012-08-01	2012-08-15	2012-08-01	2012-08-15
2430	2012-08-01	2012-08-03	2012-08-01	2012-08-03
2432	2012-08-01	2012-08-05	2012-08-01	2012-08-05
2433	2012-08-01	2012-08-06	2012-08-01	2012-08-06
2434	2012-08-01	2012-08-02	2012-08-01	2012-08-02
2436	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2439	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2441	2012-08-01	2012-08-29	2012-08-01	2012-08-29
2443	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2446	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2447	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2448	2012-08-01	2012-08-16	2012-08-01	2012-08-17
2449	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2450	2012-08-01	2012-08-05	2012-08-01	2012-08-05
2451	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2452	2012-08-01	2012-08-14	2012-08-01	2012-08-14
2453	2012-08-01	2012-08-03	2012-08-01	2012-08-03
2454	2012-08-01	2012-08-14	2012-08-01	2012-08-14
2455	2012-08-01	2012-08-08	2012-08-01	2012-08-08
2456	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2457	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2458	2012-08-01	2012-08-01	2012-08-01	2012-08-01
2459	2012-08-01	2012-08-01	2012-08-01	2012-08-01
2460	2012-08-01	2012-08-01	2012-08-01	2012-08-01

Table S1. Collar metadata. Table depicts the data on which each collar began collecting data and ceased to collected data for both GPS and accelerometry (ACC).

1000

	Total sleep time	Sleep onset time	Waking time	Sleep period duration	Sleep efficiency
Total sleep time	1	-0.61	0.65	0.87	0.57
Sleep onset time	x	1	-0.04	-0.72	-0.05
Waking time	x	x	1	0.72	0.10
Sleep period duration	x	x	x	1	0.11
Sleep efficiency	x	x	x	x	1

1001   **Table S2.** Pearson correlation coefficient between the metrics of sleep extracted from the
1002   accelerometry data. Total sleep time is correlated with all sleep metrics.
1003

Histogram of total sleep time

1004
1005   **Figure S1**. Histogram of total sleep time for the first 20 nights of the study (data prior to leopard
1006   attack
1007

	Total sleep time (Standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.03	-0.55 – 0.49
Travel distance	-0.02	-0.18 – 0.15
Time spent napping	-0.18	-0.36 – -0.01
Previous night total sleep time	-0.00	-0.14 – 0.13
Tree fidelity score	0.20	0.05 – 0.36
Relative number of baboons in tree	-0.51	-0.85 – -0.16
Minimum ambient temperature	-0.03	-0.21 – 0.13
Moon phase	0.05	-0.12 – 0.22
age: Juvenile	-0.32	-1.12 – 0.50
age: Subadult	-0.32	-0.80 – 0.14
sex: Male	0.44	-0.04 – 0.92
tree: tree2	-0.26	-1.08 – 0.56
tree: tree3	-0.15	-1.01 – 0.69
tree: tree4	-0.81	-1.30 – -0.32

33

tree: tree5	-0.24	-0.74 – 0.27
tree: tree6	0.02	-0.60 – 0.65
tree: tree7	0.10	-0.62 – 0.84
tree: tree8	-0.26	-0.75 – 0.22
tree: tree10	-0.22	-0.95 – 0.51
tree: tree11	-0.22	-0.78 – 0.32
Random Effects		
σ^2	0.53	
$\tau_{00 \ night}$	0.02	
$\tau_{00 \ tag}$	0.08	
ICC	0.16	
N $_{tag}$	18	
N $_{night}$	18	
Observations	170	
Marginal R^2 / Conditional R^2	0.340 / 0.414	

Table S3. Model output table of model total sleep time (for the first 20 days) with all numerical variables standardized

Figure S2. 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

	Total sleep time (hours)	
Predictors	*Estimates*	*CI (95%)*
Intercept	18.65	-24.20 – 63.97
Travel distance (km)	-0.01	-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
Tree fidelity score	0.60	0.15 – 1.03
Relative number of baboons in tree	-1.55	-2.58 – -0.48

34

Minimum ambient temperature (degree Celsius)	-0.03	-0.19 – 0.12
Moon phase	0.11	-0.25 – 0.48
age: Juvenile	-0.26	-0.85 – 0.38
age: Subadult	-0.25	-0.60 – 0.10
sex: Male	0.34	-0.03 – 0.72
tree: tree2	-0.20	-0.84 – 0.44
tree: tree3	-0.12	-0.79 – 0.55
tree: tree4	-0.64	-1.03 – -0.25
tree: tree5	-0.20	-0.59 – 0.19
tree: tree6	0.02	-0.48 – 0.50
tree: tree7	0.09	-0.46 – 0.64
tree: tree8	-0.22	-0.59 – 0.16
tree: tree10	-0.17	-0.74 – 0.38
tree: tree11	-0.18	-0.60 – 0.24
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	0.337 / 0.412	

Table S4. Model output table of model total sleep time (for the first 20 days) with no standardization of variables

Figure S3. 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.
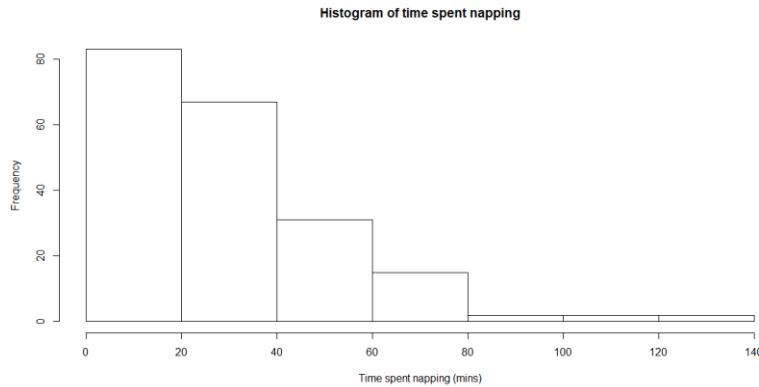
35

1027

1028
1029
1030 **Figure S4.** The conditional effect of tree identity on total sleep time. The conditional effects plotted
1031 here are from the unstandardized Bayesian linear mixed model (LMM) of total sleep time (hours).
1032

	Total sleep time (Standarized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.04	-0.55 – 0.47
Average VeDBA during day	-0.12	-0.33 – 0.12
Time spent napping	-0.13	-0.30 – 0.05
Previous night total sleep time	-0.00	-0.14 – 0.13
Tree fidelity score	0.20	0.04 – 0.36
Relative number of baboons in tree	-0.55	-0.89 – -0.20
Minimum ambient temperature	-0.04	-0.21 – 0.12
Moon phase	0.07	-0.09 – 0.23
age: Juvenile	-0.21	-1.01 – 0.59
age: Subadult	-0.26	-0.77 – 0.22
sex: Male	0.53	0.09 – 0.97
tree: tree2	-0.34	-1.18 – 0.49
tree: tree3	-0.47	-1.26 – 0.33
tree: tree4	-0.86	-1.37 – -0.35
tree: tree5	-0.28	-0.79 – 0.22
tree: tree6	0.04	-0.60 – 0.68
tree: tree7	0.08	-0.66 – 0.83
tree: tree8	-0.28	-0.77 – 0.23
tree: tree10	-0.13	-0.84 – 0.58
tree: tree11	-0.24	-0.79 – 0.31
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	0.352 / 0.416

Table S5. Model output table of model total sleep time (for the first 20 days) with all numerical variables standardized

Figure S5. Histogram of time spent napping for the first 20 days of the study (data prior to leopard attack)

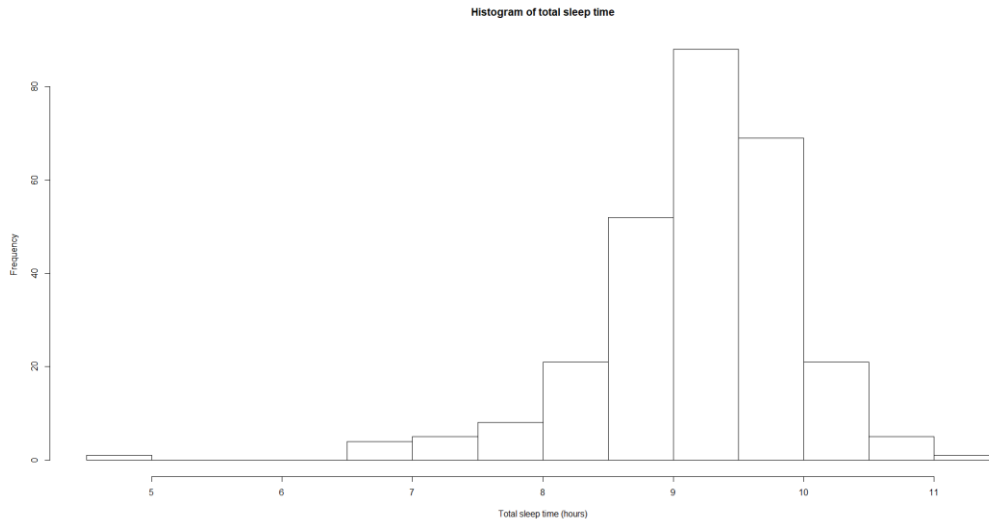|	Time spent napping (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.10	-0.49 – 0.28
Prior night total sleep time	0.05	-0.08 – 0.18
Random Effects		
σ^2	0.41	
$\tau_{00\ night}$	0.12	
$\tau_{00\ tag}$	0.51	
ICC	0.60	
N_{tag}	20	
N_{night}	19	
Observations	199	
Marginal R^2 / Conditional R^2	0.003 / 0.617	

Table S6. 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	21.22	-5.83 – 47.59
Prior night total sleep time (hours)	1.53	-1.23 – 4.42
Random Effects		
σ^2	295.93	
$\tau_{00\ night}$	25.86	
$\tau_{00\ tag}$	99.07	
ICC	0.30	
N_{tag}	20	
N_{night}	19	

Observations	199
Marginal R^2 / Conditional R^2	0.002 / 0.521

Table S7. Model output table of model of time spent napping during the day (for the first 20 days) without standardization of the variables

Histogram of total sleep time

Figure S6. Histogram of total sleep time for the entire study duration

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.24	-0.57 – 0.11
cond_night: night of leopard attack	-0.25	-0.87 – 0.39
cond_night: first night in new sleep site	-1.55	-2.18 – -0.91
cond_night: second night in new sleep site	-0.26	-0.98 – 0.44
cond_night: third night in new sleep site	0.21	-0.47 – 0.88
cond_night: remainder of nights (in original sleep site)	0.25	-0.07 – 0.56
age: Juvenile	-0.27	-1.14 – 0.59
age: Subadult	-0.36	-0.87 – 0.13
sex: Male	0.74	0.25 – 1.26
Travel distance	-0.06	-0.18 – 0.07
Time spent napping	-0.11	-0.28 – 0.05
Previous night relative total sleep time	0.15	0.04 – 0.27
Minimum ambient temperature	-0.00	-0.14 – 0.14
Moon phase	0.02	-0.12 – 0.15
Random Effects		
σ^2	0.78	
$\tau_{00\ tag}$	0.14	
ICC	0.16	
N_{tag}	20	
Observations	275	
Marginal R^2 / Conditional R^2	0.251 / 0.314	

Table S8. Model output table of model of total sleep time using data from entire study duration (including after the leopard attack) with all variables standardized
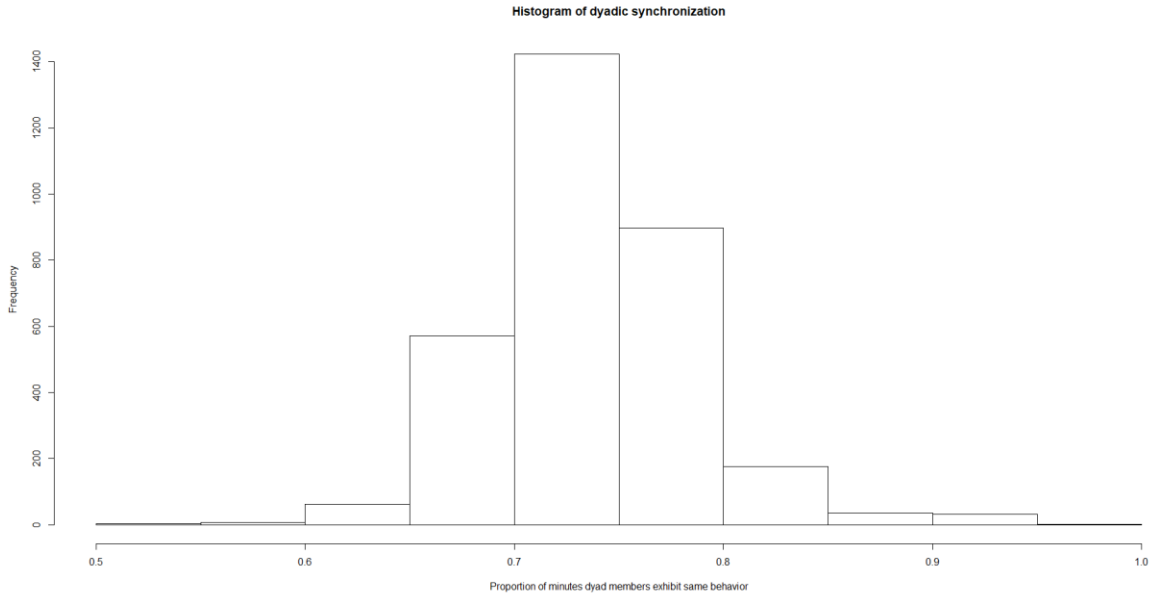
Total sleep time (hours)

Predictors	Estimates	CI (95%)
Intercept	8.43	-43.81 – 59.58
cond_night: night of leopard attack	-0.21	-0.90 – 0.48
cond_night: first night in new sleep site	-1.19	-1.88 – -0.49
cond_night: second night in new sleep site	-0.23	-0.98 – 0.48
cond_night: third night in new sleep site	0.15	-0.58 – 0.86
cond_night: remainder of nights (in original sleep site)	0.15	-0.19 – 0.48
age: Juvenile	-0.28	-0.96 – 0.39
age: Subadult	-0.31	-0.71 – 0.07
sex: Male	0.58	0.19 – 0.99
Travel distance	-0.04	-0.13 – 0.05
Time spent napping	-0.00	-0.01 – 0.00
Previous night relative total sleep time	0.00	0.00 – 0.00
Minimum ambient temperature	0.00	-0.17 – 0.19
Moon phase	0.07	-0.33 – 0.47
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	0.257 / 0.365	

Table S9. Model output table of model of total sleep time using data from entire study duration (including after the leopard attack) without standardization of variables

Figure S7. 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 S8. Histogram of the dyadic synchronization scores, which indicates the proportions of minutes between 21:00 and 05:00 during which both members of a dyad exhibited the same behavior (either sleep or wakefulness) on a given night.

	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	

Table S10. 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	

40

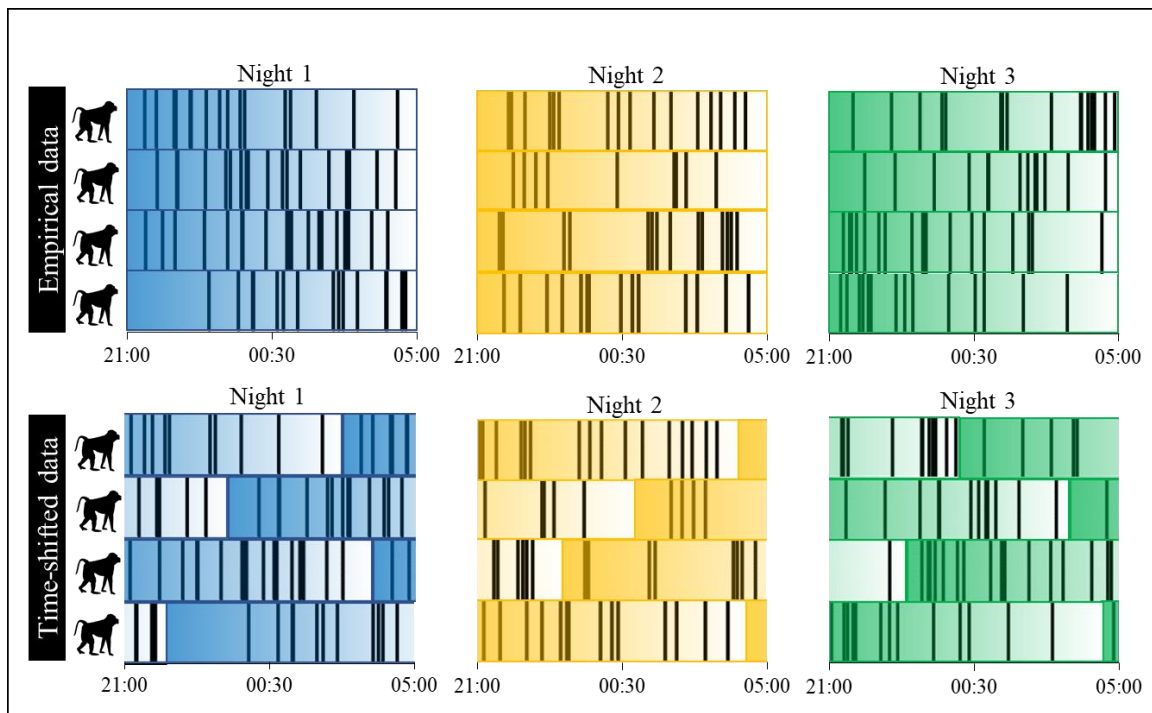| $\tau_{00\ tag1}$	0.00
$\tau_{00\ tag2}$	0.00
ICC	0.45
N $_{night}$	34
N $_{tag1}$	22
N $_{tag2}$	22
N $_{dy\_name}$	250
Observations	2997
Marginal R^2 / Conditional R^2	0.050 / 0.404

Table S11. 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

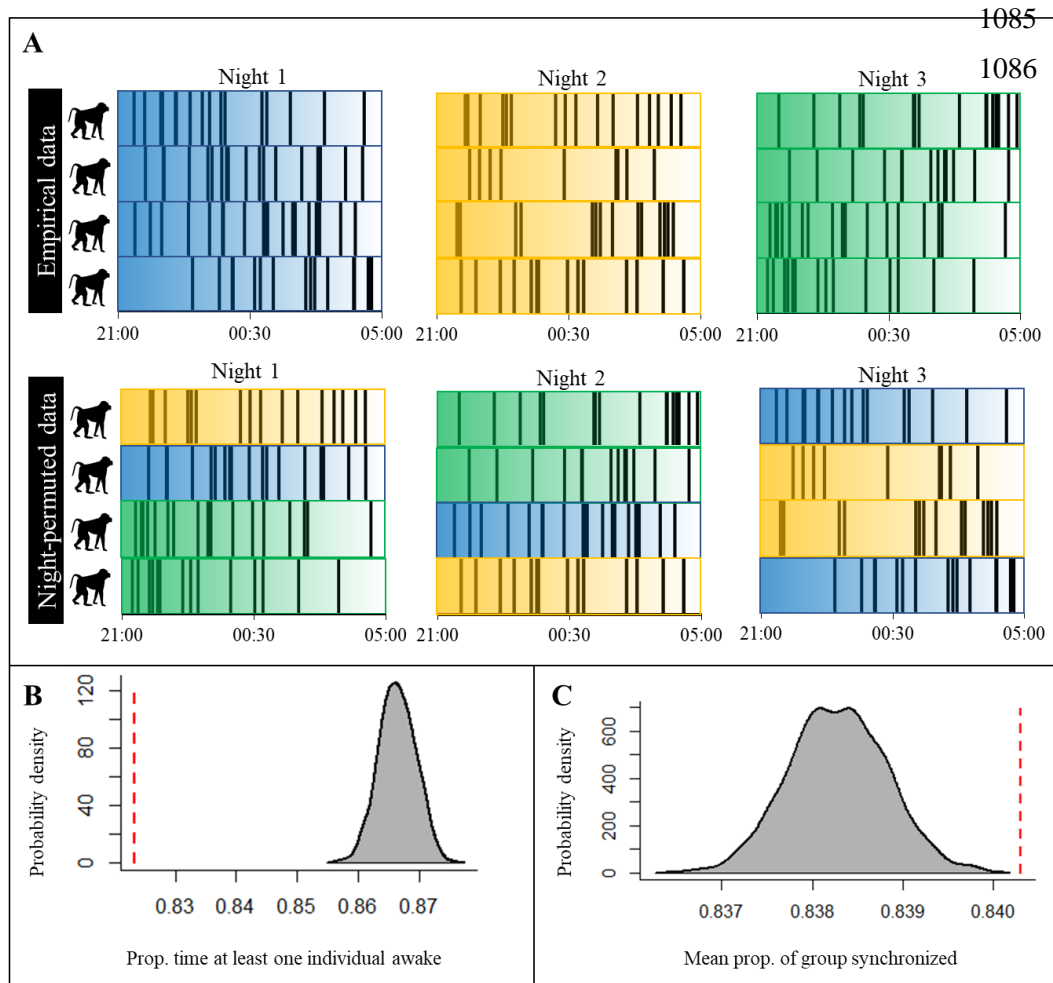**Figure S9.** A toy example of the procedure we used to test for sentinel behavior and synchronization of nighttime behavior. Each row represents a baboon's time-series of sleep and wake activity during the night, with black vertical lines indicating periods of nocturnal waking behavior. Colors correspond 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.

41

Figure S10. A) A toy example of the procedure alternative to the one presented in the main text (and represented in Figure S9) 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.

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

1112   accelerations at 56.2 Hz/axis at the beginning of every minute from 18:00 to 06:30. Accelerometry
1113   data was collected by each of these 11 collars for up to 31 days. The remaining 16 collars did not
1114   collect accelerometry data from 06:30 to 18:00, and thus we excluded data from these collars from the
1115   validation study.
1116   We down-sampled and interpolated the accelerometry data such that it matched the sampling
1117   frequency and schedule of the data collected in 2012 (i.e. the data analyzed for this manuscript). We
1118   then applied the sleep classification algorithm described in the Materials and Methods to this
1119   validation dataset.
1120   To validate the sleep classification algorithm, we performed direct behavioral observations of
1121   the baboons at their primary sleep site. We recorded the behavior of the study baboons starting when
1122   they approached their sleep site using a FLIR T1020 high-resolution infrared camera (FLIR Systems
1123   Inc., Wilsonville, OR, USA). Recordings continued into the night for as long as the camera battery
1124   allowed (average recording duration (range of recording durations): 7.4 hours (1.7 – 14.9 hours)), and
1125   we collected thermal imaging data on 21 nights. We identified individuals in the thermal imagery both
1126   in real-time, via observer narration of the recorded imagery, and post-recording, by matching
1127   movements of individuals in the thermal imagery to the GPS tracks of collared individuals.
1128   Following initial data collection, we used the commercial software Loopy (Loopbio GmbH,
1129   Austria) to score the behavior of identified individuals in the thermal imagery. Individuals' behavior
1130   was scored as "wakefulness", "resting wakefulness", or "sleep". Wakefulness refers to any behavior
1131   involving active movement (i.e. walking, running) or engaged activity (i.e. allogrooming), whereas
1132   resting wakefulness refers to behaviors that are dormant (i.e. sitting), but not in the typical sleeping
1133   posture of a baboon (sitting or lying with neck relaxed and head hung). Sustained dormant behavior in
1134   the typical sleep posture was considered sleep. Video scoring resulted in a total of 8.0 hours of
1135   behavioral observation across a total of 16 individual baboons.
1136   Synchronizing the thermal imagery data with the accelerometry data produced a validation
1137   dataset of 294 minute-epochs across six baboons that were both classified as either sleep or wakeful
1138   behavior from accelerometry, and scored as wakefulness, resting wakefulness, or sleep from direct
1139   observation. With both wakefulness and resting wakefulness representing wakeful behavior, the
1140   accelerometer-based sleep classification exhibited an accuracy of 79.9% (Table S12). Consistent with
1141   previous validation studies of the use of accelerometry in measuring sleep (Ancoli-Israel et al., 2003;
1142   de Souza et al., 2003), we found that accelerometer-based sleep classification has difficulty
1143   distinguishing resting wakefulness from sleep, and we consider this limitation in our interpretation of
1144   the results.
1145
1146

		Behavioral scoring		
		Awake		Asleep
		Wakefulness	Resting wakefulness	Sleep
Accelerometer-based sleep classification	Awake	30	85	19
	Asleep	0	40	120

1147   **Table S12.** Confusion matrix reporting the results of the validation study. Table entries represent the
1148   number of minute-epochs classified according to the accelerometer-based technique and direct
1149   behavioral observation.

1 **Supplemental Information**

2

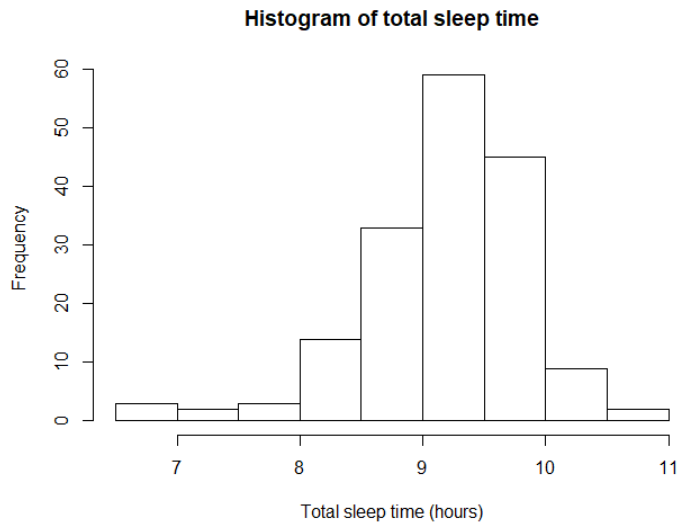| Collar #	GPS start date	GPS end date	ACC start date	ACC end date
2426	2012-08-01	2012-08-30	2012-08-01	2012-08-31
2427	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2428	2012-08-01	2012-08-15	2012-08-01	2012-08-15
2430	2012-08-01	2012-08-03	2012-08-01	2012-08-03
2432	2012-08-01	2012-08-05	2012-08-01	2012-08-05
2433	2012-08-01	2012-08-06	2012-08-01	2012-08-06
2434	2012-08-01	2012-08-02	2012-08-01	2012-08-02
2436	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2439	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2441	2012-08-01	2012-08-29	2012-08-01	2012-08-29
2443	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2446	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2447	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2448	2012-08-01	2012-08-16	2012-08-01	2012-08-17
2449	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2450	2012-08-01	2012-08-05	2012-08-01	2012-08-05
2451	2012-08-01	2012-09-02	2012-08-01	2012-09-02
2452	2012-08-01	2012-08-14	2012-08-01	2012-08-14
2453	2012-08-01	2012-08-03	2012-08-01	2012-08-03
2454	2012-08-01	2012-08-14	2012-08-01	2012-08-14
2455	2012-08-01	2012-08-08	2012-08-01	2012-08-08
2456	2012-08-01	2012-08-31	2012-08-01	2012-08-31
2457	2012-08-01	2012-09-04	2012-08-01	2012-09-04
2458	2012-08-01	2012-08-01	2012-08-01	2012-08-01
2459	2012-08-01	2012-08-01	2012-08-01	2012-08-01
2460	2012-08-01	2012-08-01	2012-08-01	2012-08-01

3 **Table S1**. Collar metadata. Table depicts the data on which each collar began collecting data and
4 ceased to collected data for both GPS and accelerometry (ACC).

5

	Total sleep time	Sleep onset time	Waking time	Sleep period duration	Sleep efficiency
Total sleep time	1	-0.61	0.65	0.87	0.57
Sleep onset time	x	1	-0.04	-0.72	-0.05
Waking time	x	x	1	0.72	0.10
Sleep period duration	x	x	x	1	0.11
Sleep efficiency	x	x	x	x	1

6 **Table S2.** Pearson correlation coefficient between the metrics of sleep extracted from the
7 accelerometry data. Total sleep time is correlated with all sleep metrics.
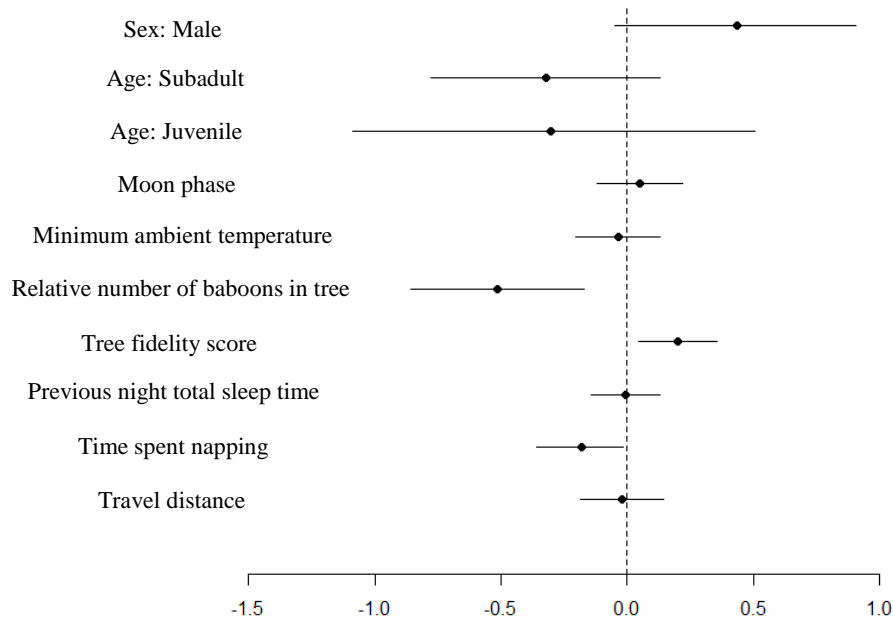
8

Histogram of total sleep time

9

10   **Figure S1**. Histogram of total sleep time for the first 20 nights of the study (data prior to leopard

11   attack

12

	Total sleep time (Standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.03	-0.55 – 0.49
Travel distance	-0.02	-0.18 – 0.15
Time spent napping	-0.18	-0.36 – -0.01
Previous night total sleep time	-0.00	-0.14 – 0.13
Tree fidelity score	0.20	0.05 – 0.36
Relative number of baboons in tree	-0.51	-0.85 – -0.16
Minimum ambient temperature	-0.03	-0.21 – 0.13
Moon phase	0.05	-0.12 – 0.22
age: Juvenile	-0.32	-1.12 – 0.50
age: Subadult	-0.32	-0.80 – 0.14
sex: Male	0.44	-0.04 – 0.92
tree: tree2	-0.26	-1.08 – 0.56
tree: tree3	-0.15	-1.01 – 0.69
tree: tree4	-0.81	-1.30 – -0.32
tree: tree5	-0.24	-0.74 – 0.27
tree: tree6	0.02	-0.60 – 0.65
tree: tree7	0.10	-0.62 – 0.84
tree: tree8	-0.26	-0.75 – 0.22
tree: tree10	-0.22	-0.95 – 0.51
tree: tree11	-0.22	-0.78 – 0.32
Random Effects		
σ^2	0.53	
$\tau_{00 \text{ night}}$	0.02	
$\tau_{00 \text{ tag}}$	0.08	
ICC	0.16	
N $_{\text{tag}}$	18	
N $_{\text{night}}$	18	
Observations	170	
Marginal R^2 / Conditional R^2	0.340 / 0.414	

2

13   **Table S3.** Model output table of model total sleep time (for the first 20 days) with all numerical
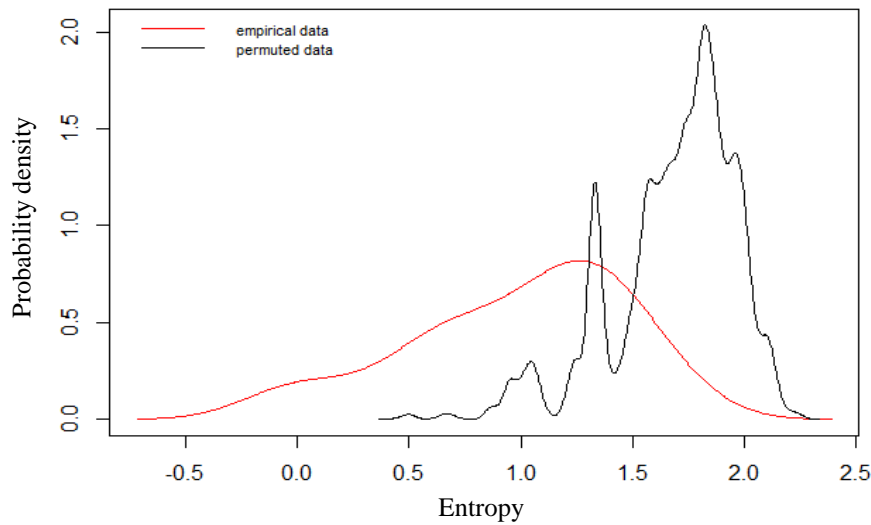14   variables standardized

15
16   **Figure S2.** Model output plot of model of total sleep time (for the first 20 days) with all numerical
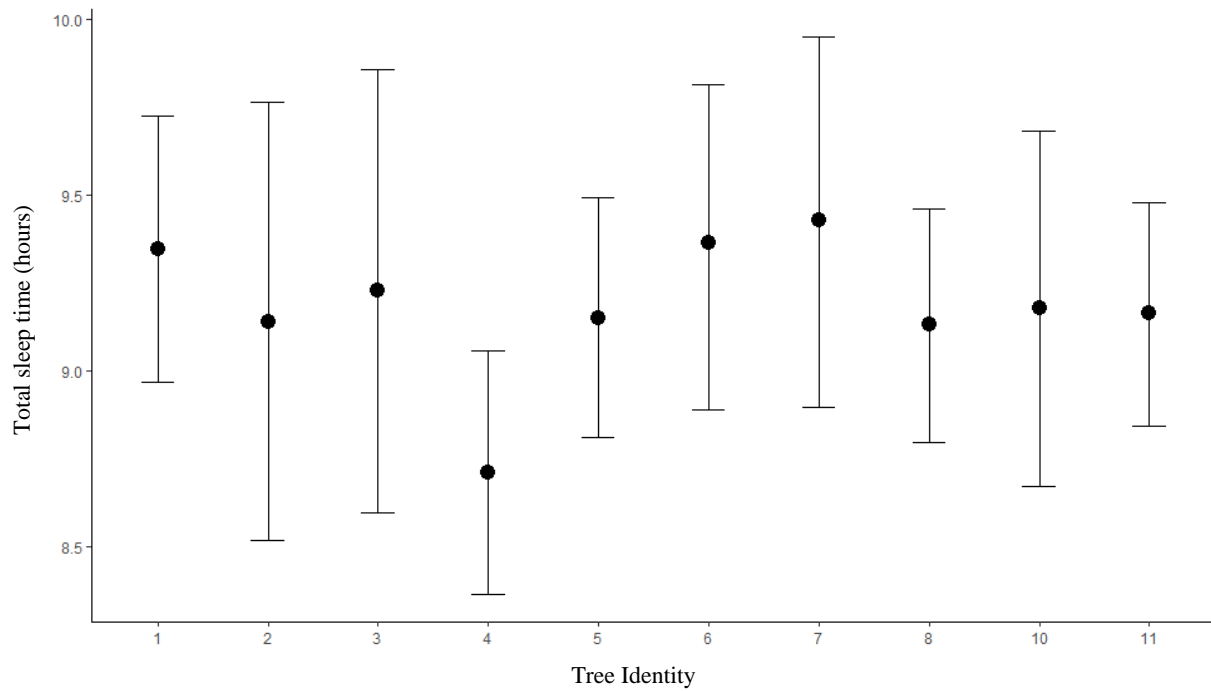17   variables standardized. The categorical variable tree is not plotted
18

	Total sleep time (hours)	
Predictors	*Estimates*	*CI (95%)*
Intercept	18.65	-24.20 – 63.97
Travel distance (km)	-0.01	-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
Tree fidelity score	0.60	0.15 – 1.03
Relative number of baboons in tree	-1.55	-2.58 – -0.48
Minimum ambient temperature (degree Celsius)	-0.03	-0.19 – 0.12
Moon phase	0.11	-0.25 – 0.48
age: Juvenile	-0.26	-0.85 – 0.38
age: Subadult	-0.25	-0.60 – 0.10
sex: Male	0.34	-0.03 – 0.72
tree: tree2	-0.20	-0.84 – 0.44
tree: tree3	-0.12	-0.79 – 0.55
tree: tree4	-0.64	-1.03 – -0.25
tree: tree5	-0.20	-0.59 – 0.19
tree: tree6	0.02	-0.48 – 0.50
tree: tree7	0.09	-0.46 – 0.64
tree: tree8	-0.22	-0.59 – 0.16
tree: tree10	-0.17	-0.74 – 0.38
tree: tree11	-0.18	-0.60 – 0.24
Random Effects		

σ^2	0.31
$\tau_{00 \text{ night}}$	0.01
$\tau_{00 \text{ tag}}$	0.05
ICC	0.17
N_{tag}	18
N_{night}	18
Observations	170
Marginal R^2 / Conditional R^2	0.337 / 0.412

Table S4. Model output table of model total sleep time (for the first 20 days) with no standardization of variables

Figure S3. 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.

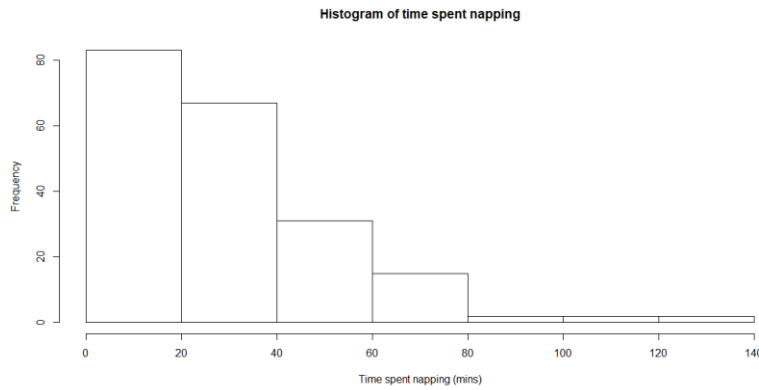**Figure S4.** The conditional effect of tree identity on total sleep time. The conditional effects plotted here are from the unstandardized Bayesian linear mixed model (LMM) of total sleep time (hours).

	Total sleep time (Standarized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.04	-0.55 – 0.47
Average VeDBA during day	-0.12	-0.33 – 0.12
Time spent napping	-0.13	-0.30 – 0.05
Previous night total sleep time	-0.00	-0.14 – 0.13
Tree fidelity score	0.20	0.04 – 0.36
Relative number of baboons in tree	-0.55	-0.89 – -0.20
Minimum ambient temperature	-0.04	-0.21 – 0.12
Moon phase	0.07	-0.09 – 0.23
age: Juvenile	-0.21	-1.01 – 0.59
age: Subadult	-0.26	-0.77 – 0.22
sex: Male	0.53	0.09 – 0.97
tree: tree2	-0.34	-1.18 – 0.49
tree: tree3	-0.47	-1.26 – 0.33
tree: tree4	-0.86	-1.37 – -0.35
tree: tree5	-0.28	-0.79 – 0.22
tree: tree6	0.04	-0.60 – 0.68
tree: tree7	0.08	-0.66 – 0.83
tree: tree8	-0.28	-0.77 – 0.23
tree: tree10	-0.13	-0.84 – 0.58
tree: tree11	-0.24	-0.79 – 0.31
Random Effects		
σ^2	0.55	
$\tau_{00\ night}$	0.02	
$\tau_{00\ tag}$	0.07	
ICC	0.13	

5

N_{tag}	18
N_{night}	18
Observations	178
Marginal R^2 / Conditional R^2	0.352 / 0.416

Table S5. Model output table of model total sleep time (for the first 20 days) with all numerical variables standardized

Histogram of time spent napping

Figure S5. Histogram of time spent napping for the first 20 days of the study (data prior to leopard attack)

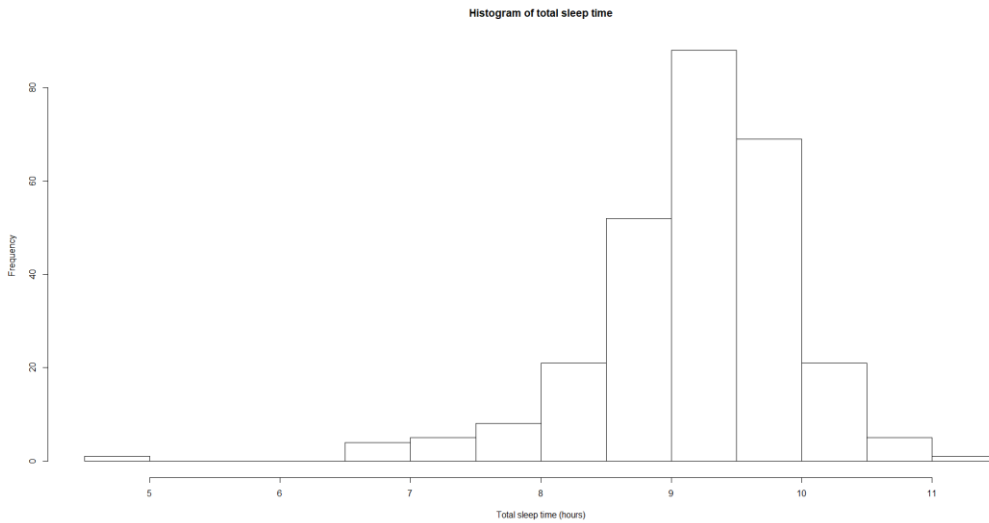|	Time spent napping (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.10	-0.49 – 0.28
Prior night total sleep time	0.05	-0.08 – 0.18
Random Effects		
σ^2	0.41	
$\tau_{00\ night}$	0.12	
$\tau_{00\ tag}$	0.51	
ICC	0.60	
N_{tag}	20	
N_{night}	19	
Observations	199	
Marginal R^2 / Conditional R^2	0.003 / 0.617	

Table S6. 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	21.22	-5.83 – 47.59
Prior night total sleep time (hours)	1.53	-1.23 – 4.42
Random Effects		
σ^2	295.93	
$\tau_{00\ night}$	25.86	
$\tau_{00\ tag}$	99.07	
ICC	0.30	
N_{tag}	20	
N_{night}	19	
Observations	199	

Marginal R^2 / Conditional R^2	0.002 / 0.521

48 **Table S7.** Model output table of model of time spent napping during the day (for the first 20 days)
49 without standardization of the variables
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51
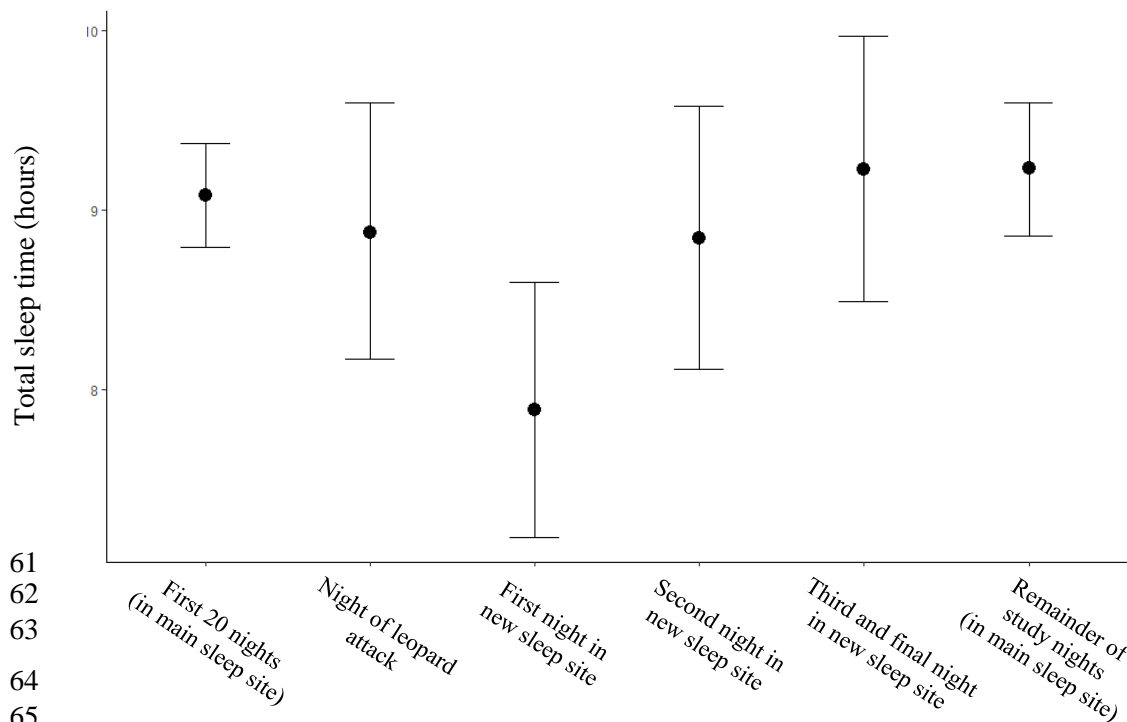52 **Figure S6.** Histogram of total sleep time for the entire study duration
53
54

	Total sleep time (standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.24	-0.57 – 0.11
cond_night: night of leopard attack	-0.25	-0.87 – 0.39
cond_night: first night in new sleep site	-1.55	-2.18 – -0.91
cond_night: second night in new sleep site	-0.26	-0.98 – 0.44
cond_night: third night in new sleep site	0.21	-0.47 – 0.88
cond_night: remainder of nights (in original sleep site)	0.25	-0.07 – 0.56
age: Juvenile	-0.27	-1.14 – 0.59
age: Subadult	-0.36	-0.87 – 0.13
sex: Male	0.74	0.25 – 1.26
Travel distance	-0.06	-0.18 – 0.07
Time spent napping	-0.11	-0.28 – 0.05
Previous night relative total sleep time	0.15	0.04 – 0.27
Minimum ambient temperature	-0.00	-0.14 – 0.14
Moon phase	0.02	-0.12 – 0.15
Random Effects		
σ^2	0.78	
$\tau_{00\ tag}$	0.14	
ICC	0.16	
N $_{tag}$	20	
Observations	275	
Marginal R^2 / Conditional R^2	0.251 / 0.314	

55 **Table S8.** Model output table of model of total sleep time using data from entire study duration
56 (including after the leopard attack) with all variables standardized
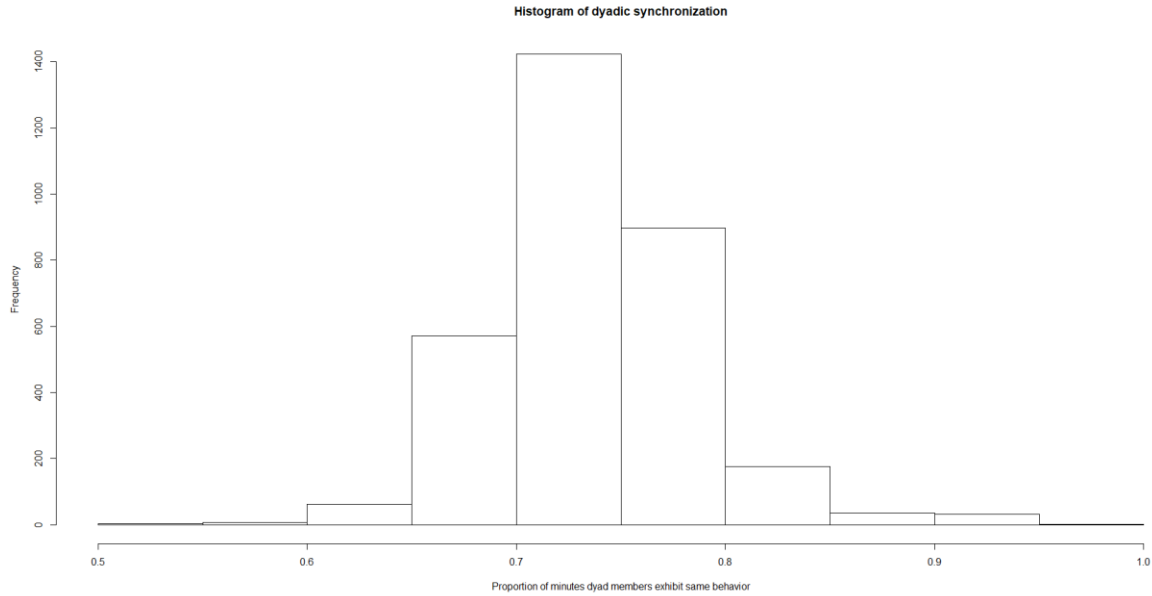57

	Total sleep time (hours)	
Predictors	*Estimates*	*CI (95%)*

7

Intercept	8.43	-43.81 – 59.58
cond_night: night of leopard attack	-0.21	-0.90 – 0.48
cond_night: first night in new sleep site	-1.19	-1.88 – -0.49
cond_night: second night in new sleep site	-0.23	-0.98 – 0.48
cond_night: third night in new sleep site	0.15	-0.58 – 0.86
cond_night: remainder of nights (in original sleep site)	0.15	-0.19 – 0.48
age: Juvenile	-0.28	-0.96 – 0.39
age: Subadult	-0.31	-0.71 – 0.07
sex: Male	0.58	0.19 – 0.99
Travel distance	-0.04	-0.13 – 0.05
Time spent napping	-0.00	-0.01 – 0.00
Previous night relative total sleep time	0.00	0.00 – 0.00
Minimum ambient temperature	0.00	-0.17 – 0.19
Moon phase	0.07	-0.33 – 0.47
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	0.257 / 0.365	

58 **Table S9.** Model output table of model of total sleep time using data from entire study duration
59 (including after the leopard attack) without standardization of variables
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66 **Figure S7.** The conditional effect of night condition on total sleep time. The conditional effects
67 presented here are from the unstandardized model of total sleep time.
68

Figure S8. Histogram of the dyadic synchronization scores, which indicates the proportions of minutes between 21:00 and 05:00 during which both members of a dyad exhibited the same behavior (either sleep or wakefulness) on a given night.

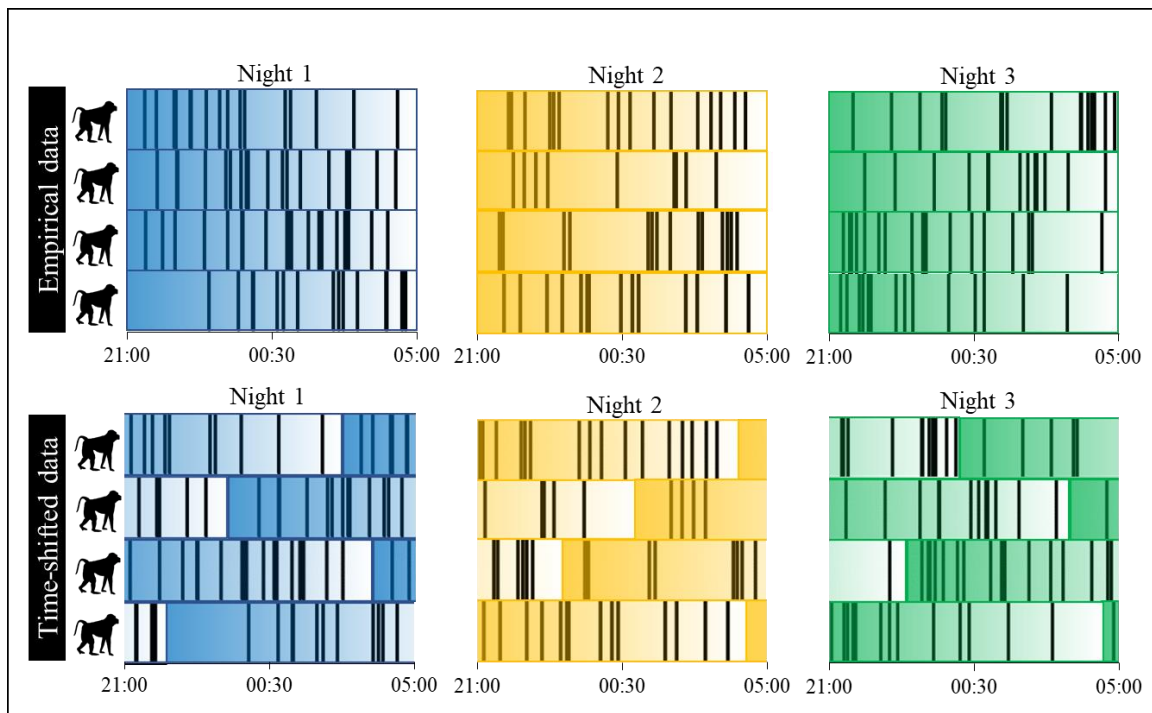|	Proportion of minutes synchronized (Standardized)	
Predictors	*Estimates*	*CI (95%)*
Intercept	-0.21	-0.45 – 0.03
Occupying same tree	0.56	0.47 – 0.64
Random Effects		
σ^2	0.60	
$\tau_{00\ dy\_name}$	0.14	
$\tau_{00\ night}$	0.19	
$\tau_{00\ tag1}$	0.08	
$\tau_{00\ tag2}$	0.09	
ICC	0.45	
N $_{night}$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

Table S10. 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
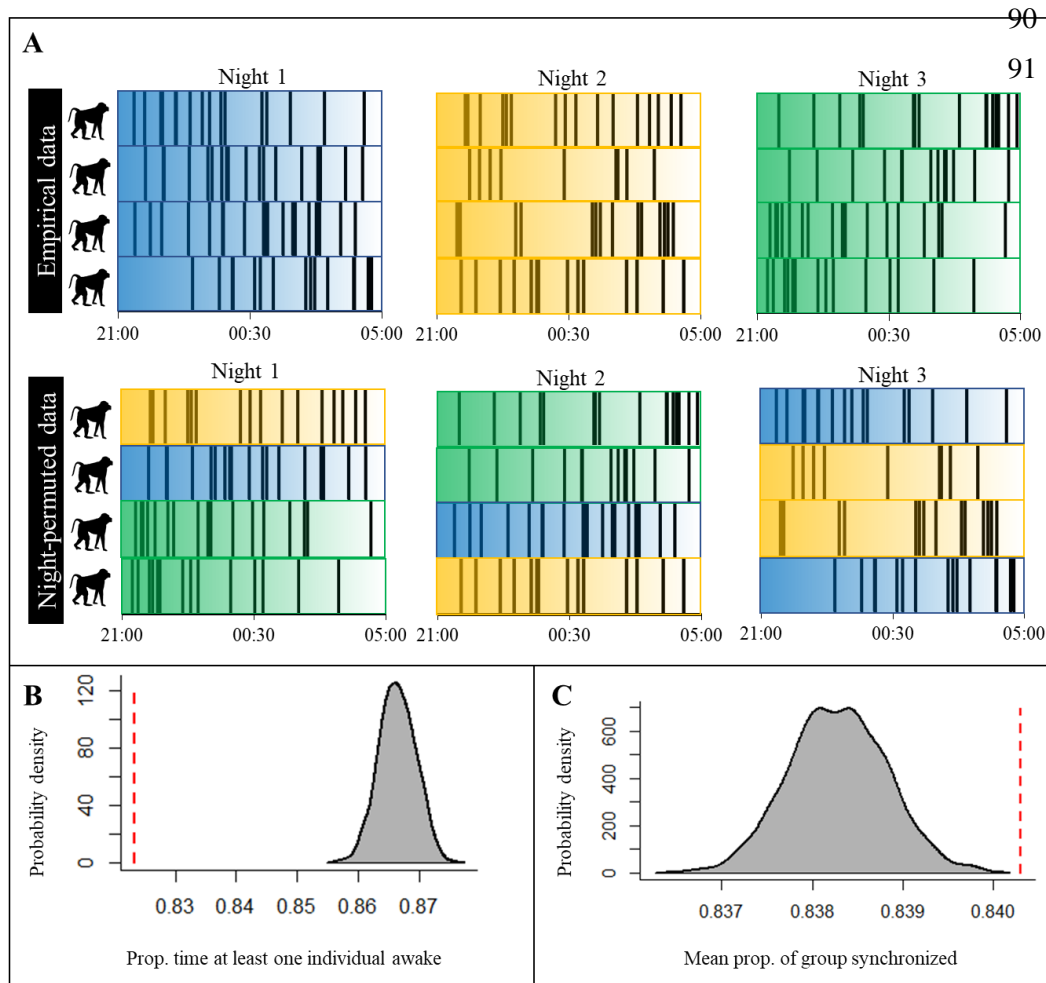
	Proportion of minutes synchronized	
Predictors	*Estimates*	*CI (95%)*
Intercept	0.73	0.71 – 0.74
Occupying same tree	0.03	0.02 – 0.03
Random Effects		
σ^2	0.00	
$\tau_{00\ dy\_name}$	0.00	
$\tau_{00\ night}$	0.00	

$\tau_{00 \ tag1}$	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 R² / Conditional R²	0.050 / 0.404

Table S11. 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

Figure S9. 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 S10. A) A toy example of the procedure alternative to the one presented in the main text (and represented in Figure S9) 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.

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

117   accelerations at 56.2 Hz/axis at the beginning of every minute from 18:00 to 06:30. Accelerometry
118   data was collected by each of these 11 collars for up to 31 days. The remaining 16 collars did not
119   collect accelerometry data from 06:30 to 18:00, and thus we excluded data from these collars from the
120   validation study.
121   We down-sampled and interpolated the accelerometry data such that it matched the sampling
122   frequency and schedule of the data collected in 2012 (i.e. the data analyzed for this manuscript). We
123   then applied the sleep classification algorithm described in the Materials and Methods to this
124   validation dataset.
125   To validate the sleep classification algorithm, we performed direct behavioral observations of
126   the baboons at their primary sleep site. We recorded the behavior of the study baboons starting when
127   they approached their sleep site using a FLIR T1020 high-resolution infrared camera (FLIR Systems
128   Inc., Wilsonville, OR, USA). Recordings continued into the night for as long as the camera battery
129   allowed (average recording duration (range of recording durations): 7.4 hours (1.7 – 14.9 hours)), and
130   we collected thermal imaging data on 21 nights. We identified individuals in the thermal imagery both
131   in real-time, via observer narration of the recorded imagery, and post-recording, by matching
132   movements of individuals in the thermal imagery to the GPS tracks of collared individuals.
133   Following initial data collection, we used the commercial software Loopy (Loopbio GmbH,
134   Austria) to score the behavior of identified individuals in the thermal imagery. Individuals' behavior
135   was scored as "wakefulness", "resting wakefulness", or "sleep". Wakefulness refers to any behavior
136   involving active movement (i.e. walking, running) or engaged activity (i.e. allogrooming), whereas
137   resting wakefulness refers to behaviors that are dormant (i.e. sitting), but not in the typical sleeping
138   posture of a baboon (sitting or lying with neck relaxed and head hung). Sustained dormant behavior in
139   the typical sleep posture was considered sleep. Video scoring resulted in a total of 8.0 hours of
140   behavioral observation across a total of 16 individual baboons.
141   Synchronizing the thermal imagery data with the accelerometry data produced a validation
142   dataset of 294 minute-epochs across six baboons that were both classified as either sleep or wakeful
143   behavior from accelerometry, and scored as wakefulness, resting wakefulness, or sleep from direct
144   observation. With both wakefulness and resting wakefulness representing wakeful behavior, the
145   accelerometer-based sleep classification exhibited an accuracy of 79.9% (Table S12). Consistent with
146   previous validation studies of the use of accelerometry in measuring sleep (Ancoli-Israel et al., 2003;
147   de Souza et al., 2003), we found that accelerometer-based sleep classification has difficulty
148   distinguishing resting wakefulness from sleep, and we consider this limitation in our interpretation of
149   the results.
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		Behavioral scoring		
		Awake		Asleep
		Wakefulness	Resting wakefulness	Sleep
Accelerometer-based sleep classification	Awake	30	85	19
	Asleep	0	40	120

152 **Table S12.** Confusion matrix reporting the results of the validation study. Table entries represent the
153 number of minute-epochs classified according to the accelerometer-based technique and direct
154 behavioral observation.