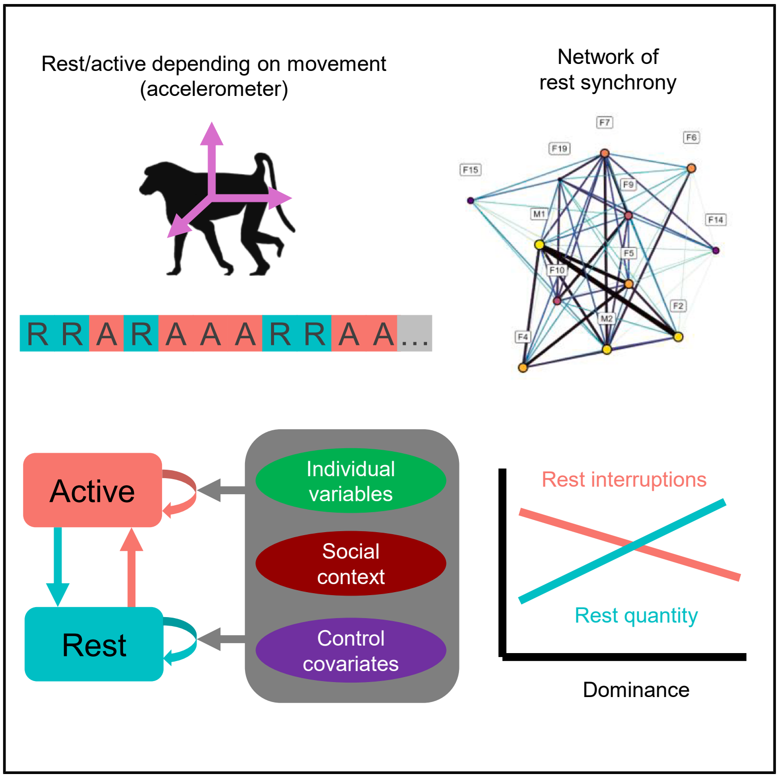
Report

Current Biology

Dominant baboons experience more interrupted and less rest at night

Graphical abstract



Highlights

- Baboons of higher social dominance have more interrupted and less nighttime rest
- Baboons of similar social dominance rank are more synchronized
- Baboons of similar dominance rank influence each other's rest behavior more
- Spatial proximity probably underlies rest synchrony and influence

Authors

Marco Fele, Charlotte Christensen,
Anna M. Bracken, ...,
Marina Papadopoulou, Ines Fürtbauer,
Andrew J. King

Correspondence

2252927@swansea.ac.uk (M.F.),
a.j.king@swansea.ac.uk (A.J.K.)

In brief

Fele et al. investigate nighttime rest in wild chacma baboons. They show that individuals synchronize their rest, but dominant baboons rest less and with more interruptions, likely because higher-ranked individuals have more nearby group members, which increases the chances of being disturbed.

Fele et al., 2026, Current Biology *36*, 209–216
January 5, 2026
https://doi.org/10.1016/j.cub.2025.10.028

CellPress

Current Biology

CellPress
OPEN ACCESS

Report

Dominant baboons experience more interrupted and less rest at night

Marco Fele,[1,5,*] Charlotte Christensen,[2] Anna M. Bracken,[3] M. Justin O' Riain,[4] Miguel Lurgi,[1] Marina Papadopoulou,[1] Ines Fürtbauer,[1] and Andrew J. King[1,*]

[1]Biosciences, Faculty of Science and Engineering, Swansea University, Singleton Park, Swansea SA2 8PP, UK
[2]Department of Evolutionary Biology and Environmental Science, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
[3]School of Biodiversity, One Health and Veterinary Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
[4]Institute for Communities and Wildlife in Africa, Biological Sciences Department, University of Cape Town, University Ave N, Cape Town 7701, South Africa
[5]Lead contact
*Correspondence: 2252927@swansea.ac.uk (M.F.), a.j.king@swansea.ac.uk (A.J.K.)
https://doi.org/10.1016/j.cub.2025.10.028

SUMMARY

Sleep is a fundamental biological process.[1,2] The amount and quality of sleep individuals get can impact various aspects of human and non-human animal health,[1] ultimately affecting fitness.[3] For wild animals that sleep in groups, individuals may disturb one another's sleep,[4,5] but this aspect of social sleep has been understudied due to methodological challenges.[6–8] Here, using nighttime rest (absence of bodily movements) as a proxy for sleep, we test the hypothesis that an individual's social dominance affects nighttime rest in a troop of wild, highly hierarchical[8,9] chacma baboons (*Papio ursinus*). First, we show that the troop's nighttime rest (determined by 40 Hz acceleration data) is highly synchronized. Next, we link nighttime rest dynamics to daytime spatial networks and dominance hierarchy (from 1 Hz GPS data and direct observations). We show that baboon nighttime states (activity and rest) are more synchronized between similarly ranked individuals and, unexpectedly, that more dominant baboons experience more interrupted and less nighttime rest than lower-ranked baboons. We propose that this hierarchy effect is explained by higher-ranked baboons resting closer to more group members, which leads them to exert a greater influence on each other's nighttime behavior compared with lower-ranked individuals. Our study provides the first evidence for the impact of social hierarchies on aspects of sleep in a wild primate, suggesting that dominance status may impose trade-offs between social rank and the quality and quantity of sleep.

RESULTS

For group-living animals that sleep together, such as humans (*Homo sapiens*), communal sleep promotes safety[9] but the restlessness of nearby individuals can disturb sleep.[5,10] Similar disruptions occur in other social primates like baboons (*Papio anubis*)[4] and macaques (*Macaca fuscata yakui*),[11] leading to synchronized sleep and wake behavior among group members. Because it is challenging to conduct electrophysiological recordings[12,13] to study primate sleep in the wild, we used nighttime rest (i.e., the absence of physical activity based upon accelerometer data[14]) as a proxy for sleep. We found that individuals spent (mean ± SD) 9.0 ± 0.19 hours resting and 1.37 ± 0.19 hours active each night (Figure 1A) and were active earlier in the morning and rested later in the evening with increasing day length (generalized linear mixed model [GLMM], beta: −0.01, $p < 0.001$).

Baboons rested simultaneously for approximately one third of the night (2.78 ± 0.69 hours per night), which is more time than would be expected if all individuals behaved independently (Chi-square goodness of fit: $p < 0.001$; Figure 1B). By modeling the resting and active states of individuals as a Markov chain (Figure 1C), we tested whether (1) rest persistence, $\hat{p}_{R\to R}$ (i.e., the probability of resting in successive timesteps); (2) restlessness, $\hat{p}_{A\to A}$, (i.e., the probability of being active in successive timesteps); and (1) rest quantity, $\hat{p}_{R}$ (the overall probability of resting during the night), were predicted by the number of other resting individuals. We found that when more baboons are at rest, individuals' rest persistence $\hat{p}_{R\to R}$ increased (GLMM: beta: 0.20, $p < 0.001$) and restlessness $\hat{p}_{A\to A}$ decreased (GLMM: beta: −0.06, $p < 0.001$), resulting in an overall increase in rest quantity $\hat{p}_{R}$ (Figure 1D) (full model outputs in Table S1). Because we calculated probabilities on a second-by-second basis, these effects can "stack up" during the night. For example, a 99% compared with 100% rest persistence corresponds to, on average, 288 more interruptions over 8 h. In all analyses, we controlled for the effects of nighttime rainfall, temperature, and moon illumination, as well as the temporal autocorrelation in rest across nights (Table S1).

Dominant baboons have more interrupted and less nighttime rest

We found that baboons of higher dominance rank had lower rest persistence $\hat{p}_{R\to R}$ (GLMM: beta: −3.52, $p < 0.001$) and higher

Current Biology *36*, 209–216, January 5, 2026 © 2025 The Authors. Published by Elsevier Inc.

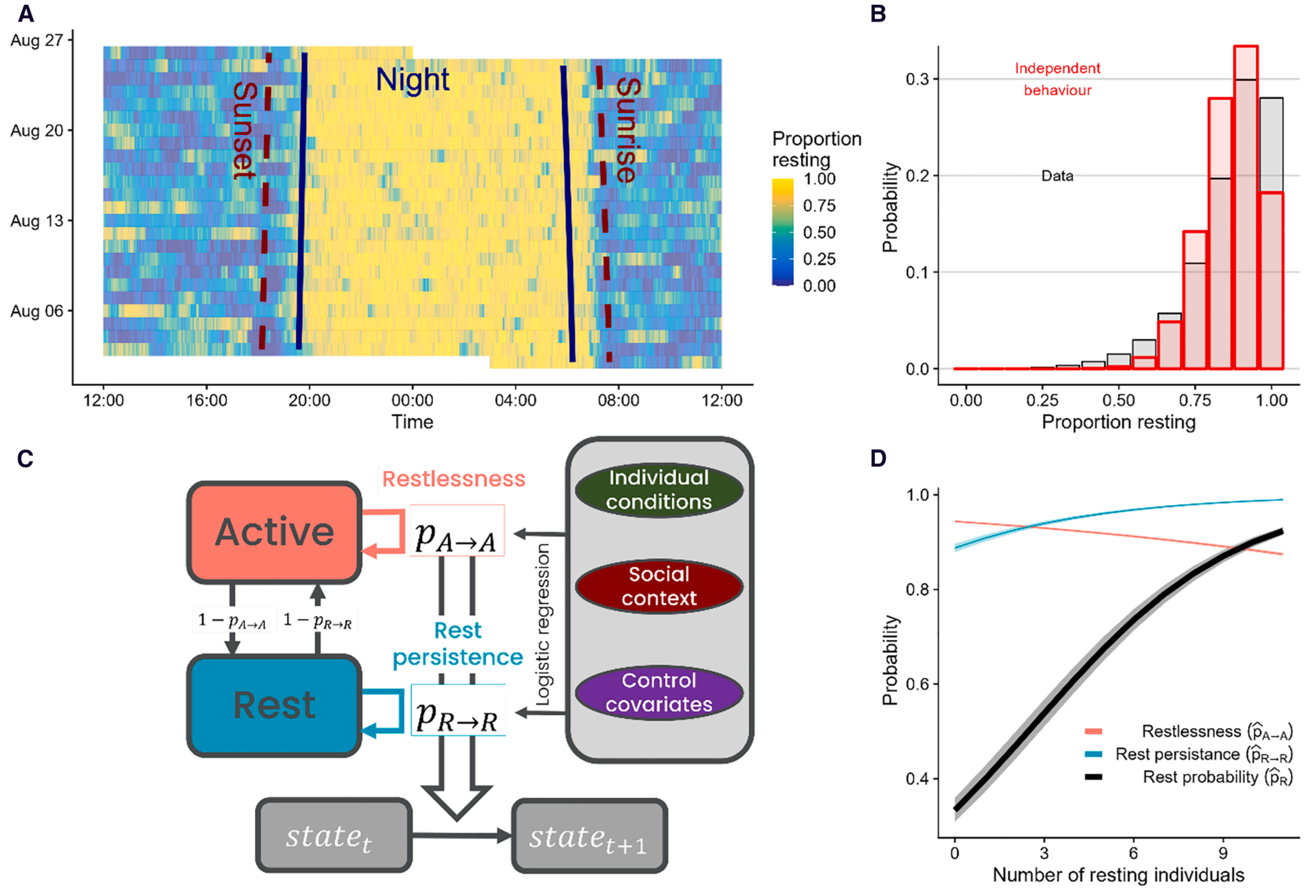


Figure 1. Baboon nighttime rest dynamics

(A) Proportion of baboons (wearing tracking collars) that are at rest (see STAR methods) over days (*y* axis) and time (*x* axis). Night darkness, sunrise, and sunset are indicated by vertical lines.

(B) Probability of rest observed (from data) and predicted from a null model where we assume individuals behave independently (see STAR methods).

(C) Using the probability of baboons switching between active and rest states, we model rest persistence, $\widehat{p}_{R\to R}$ (i.e., the probability of resting in successive timesteps), and restlessness, $\widehat{p}_{A\to A}$, (i.e., the probability of being active in successive timesteps), which we use to calculate overall rest quantity (the overall probability of resting during the night). See STAR Methods for full details and Figure S2 for additional information about frequency distributions for lengths of continuous behaviors. In all analyses, we control for individual, social, and environmental factors (see Table S1).

(D) Applying the framework shown in (C), we find that when more baboons are resting at night, an individual's rest persistence increases, restlessness decreases, and rest quantity increases. Note that the number of resting individuals (*x* axis) excludes the focal individual. Shaded areas indicate standard error.

restlessness $\widehat{p}_{A\to A}$ (GLMM: beta: 2.32, $p < 0.001$), resulting in them getting overall less rest $\widehat{p}_R$ (Figure 2A), with ∼6 hours of rest predicted for the most dominant individual compared with ∼8.5 hours for the most subordinate individual. To understand this hierarchy effect, we considered *how* baboons may influence each other's rest at night. The disruptive effects of others' activity during group sleep may not be experienced equally by all members, particularly in socially hierarchical groups where dominance can influence the number or identity of neighbours[15,16] or sleeping positions.[17] We therefore tested whether dominance mediated individuals' responses to their social environment and tested for an interaction between dominance and the number of other resting individuals. We found a positive interaction for rest persistence $\widehat{p}_{R\to RS}$ (GLMM; beta: 0.04, $p < 0.001$) and a negative interaction for restlessness $\widehat{p}_{A\to A}$ (GLMM; beta: −0.04, $p < 0.001$), indicating stronger synchrony effects among dominant individuals (Figure 2B).

Visualizing the observed synchrony in state (active or rest) for pairs of baboons (Figure 2C) suggests that individuals of similar dominance have a higher probability of being in the same state, and this was supported by our model (interaction $\widehat{p}_{R\to R}$: 4.97, p value < 0.001; interaction $\widehat{p}_{A\to A}$: −3.11 p value < 0.001). We therefore performed a cross-correlation analysis[18–20] of the behavioral time series (state: active or rest) for each pair of individuals. Cross-correlation considers both activity and rest and does not depend on the time spent in each state but rather on their temporal distribution.[21] The maximum cross-correlation was higher between dominant individuals (GLMM: beta: 0.26, lower credible interval (CI) = 0.02, upper CI = 0.48, Figure 2D), with more dominant individuals being on average the "leaders" in the behavioral coupling of states (Figure 2E). This translates into dominant individuals having greater influence on others' state (positive shifts of peak cross-correlation) (GLMM, beta: 0.44, $p = 0.02$ for lead/follow response; Figure 2F). Furthermore,

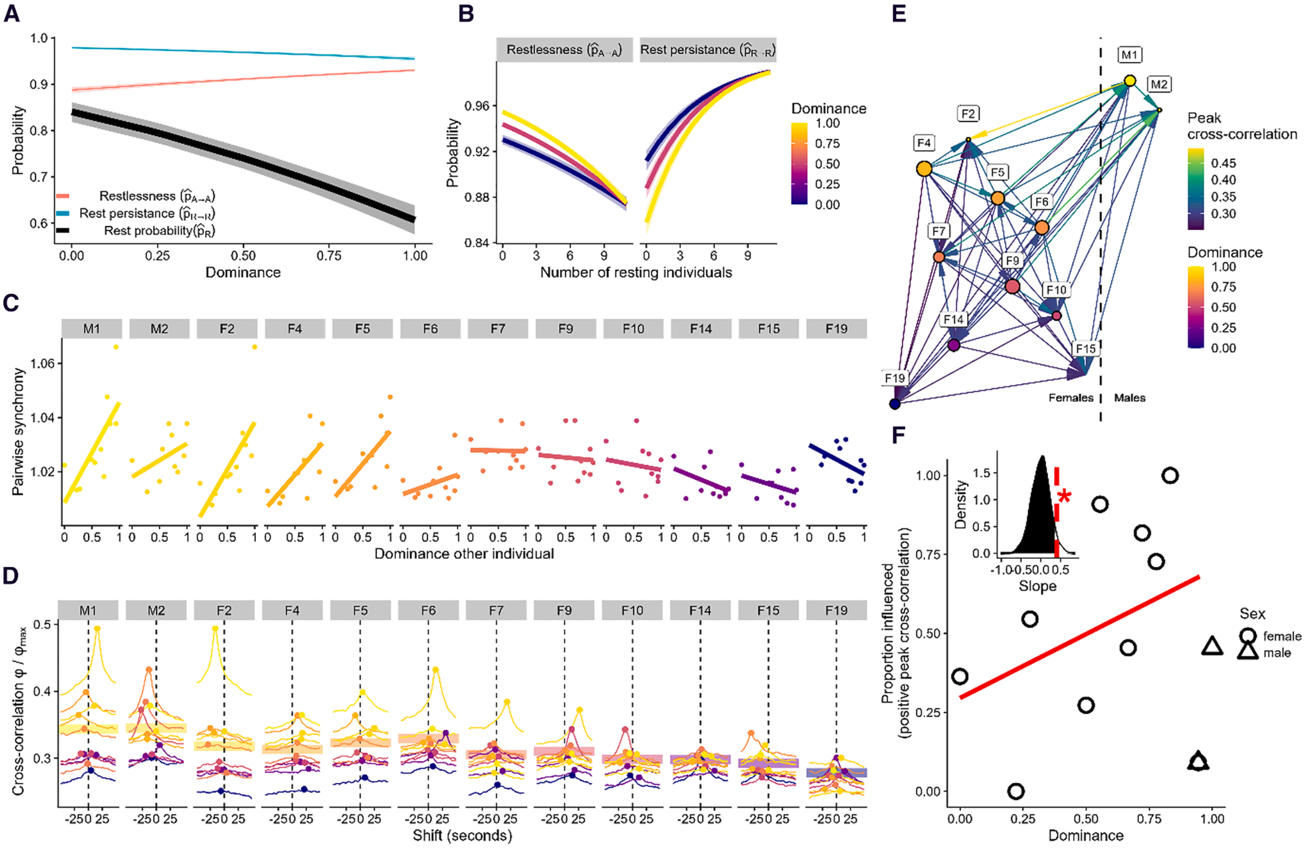


Figure 2. Dominance effects on baboons' nighttime rest

(A) Higher-ranked baboons have poorer rest persistence, $\widehat{p}_{R\to R}$ (i.e., the probability of resting in successive timesteps); are more likely to stay awake, $\widehat{p}_{A\to A}$, (i.e., the probability of being active in successive timesteps); and, as a result, have lower rest quantity, $\widehat{p}_R$ (the overall probability of resting during the night). Also see Figure S1; Table S1 for full model output and predictions. Shaded areas indicate standard errors.

(B) With more baboons at rest (*x* axis), there is a higher probability of staying at rest ($\widehat{p}_{R\to R}$) and lower probability of staying active ($\widehat{p}_{A\to A}$); the higher the dominance, the stronger the effect. Table S2 provides full model outputs and Figure S3 shows model predictive error. Shaded areas indicate standard errors.

(C) Pairwise synchrony in state (active or rest) for each baboon as a function of the dominance of a paired individual. Baboons are ordered from left to right, according to dominance. Raw data are shown with a linear regression fitted line to illustrate the direction of the relationship—showing that similarly ranked baboons are synchronized in state.

(D) Cross-correlation of a baboon's state with the state of others (ordered left to right by dominance). The strength of the cross-correlation (*y* axis) shows how similar the two baboons' states are. The time shift (*x* axis) indicates whether other baboons change state before or after the focal baboon. Horizontal lines indicate average individual cross-correlation strength.

(E) Dominant baboons have greater influence on others' state; we present a network visualization of the effect shown in (D), where dominant baboons tend to have higher correlation with other high-ranked baboons (and tend to lead transitions). Individual baboons are represented as nodes, colored by dominance, and links between two nodes represents the strength of the peak cross-correlation in state. Horizontal lines indicate the average peak-cross correlation.

(F) Correlation between individual dominance and the proportion of influenced baboons. Inset shows the distribution of dominance effects under a null model and the observed significant relationship (dotted line). STAR Methods provide full details.

females influence others' state more than males (GLMM, beta: -0.42, $p = 0.01$), but note that our sample size for males is $n = 2$.

Why do dominant baboons have less nighttime rest?

Together, our results show that more dominant baboons exert greater influence on each other's nighttime behavior compared with lower-ranked individuals. Could a simple mechanism based on spatial proximity[4] explain these dynamics? We found that baboons of similar dominance rank are closer to each other during the daytime (GLMM, beta: 0.37, lower CI = 0.13, upper CI = 0.62, Figure 3A), and pairs of baboons that are closer to each other in the daytime have higher correlation in their transition between rest and active states at night (GLMM, beta: 0.83, lower CI = 0.61, upper CI = 1.03; Figure 3B; Table S2). Furthermore, dominant baboons are more central (higher eigenvector centrality) in both daytime proximity networks and the predicted rest influence network (Figure 2E) (GLMM proximity, beta: 0.67, $p = 0.002$; GLMM influence, beta: 0.15, $p = 0.04$). We therefore propose, as a plausible explanation, that dominant baboons have more and closer neighbors at nighttime and thus end up waking and being woken by other baboons more frequently (Figure 2C).

DISCUSSION

We find evidence of direct social influence on baboons' nighttime rest, indicating that more dominant individuals have a

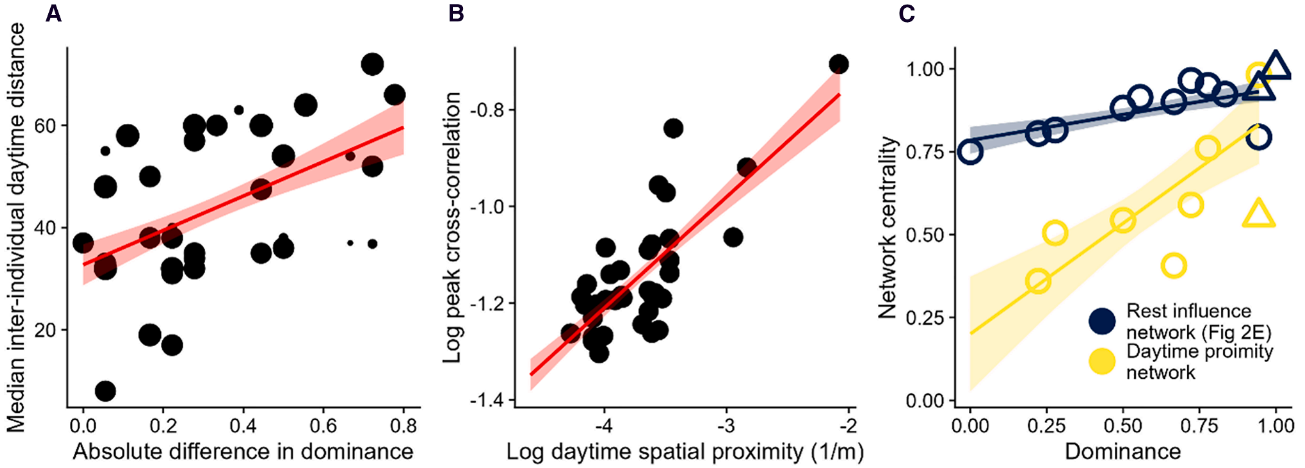


Figure 3. Proximity networks and nighttime rest influence

(A) Baboons of similar rank (*x* axis) spend more time closer to each other (*y* axis). Raw data are shown, with point size indicating sample size for estimating median daytime pairwise distance, and a linear relationship (line) and standard error (shaded area) is fitted for illustration.

(B) Baboons that are closer to each other during the daytime (*x* axis) have a higher correlation in their transition between rest and active states at night (*y* axis). Raw data are shown, with point size indicating sample size, and a linear relationship (line) and standard error (shaded area) is fitted for illustration.

(C) Higher-ranked baboons (*x* axis) have greater eigenvector network centrality in daytime proximity networks and nighttime rest influence networks (*y* axis). Raw data are shown (triangles indicate males), and a linear relationship (line) and standard error (shaded area) is fitted for illustration. Individuals for which we have GPS and accelerometer data are in Table S2.

greater effect on each other's behavior. This effect is found when controlling for night-level environmental factors. Although we do not measure continuous environmental variation overnight (e.g., external noise sources) that can confound pairwise synchrony, this is partially overcome by the cross-correlation analysis (rest influence), which checks for consistent time delays in behavioral states between individuals. Furthermore, rest influence matches daytime spatial proximity patterns. We therefore propose that nighttime proximity mirrors daytime associations (influence will occur between spatially close individuals), as seen in howler monkeys (*Alouatta caraya*),[22] and dominant individuals occupy more central sleeping positions or sleep in bigger subgroups with more nearby neighbors, as observed in sleeping lemurs (*Microcebus murinus*).[23,24] Such association patterns could lead to higher-ranked individuals exerting greater influence on each other's nighttime behavior compared with lower-ranked individuals, resulting in more dominant baboons experiencing less sleep.

Despite the recognized importance of social hierarchies and structure on animal lives during the daytime,[25–29] we are aware of only two studies that have investigated dominance rank effects on sleep: in freely moving mice, *Mus musculus*,[30] and captive gelada baboon, *Theropithecus gelada*.[31] In mice, authors found that socially dominant individuals had overall reduced slow-wave activity and more fragmented sleep but were unable to identify a cause for these differences. In the gelada study, within females (n = 3) and juveniles (n = 3), the highest-ranked individuals slept less, and the authors suggest this is because they are more alert. Taking nighttime rest as a proxy for sleep, our findings suggest a different explanation, namely that dominance affects sleep indirectly by influencing the number and identity of nearby resting individuals. In other words, social disruption, mediated by spatial proximity, may be the primary driver of sleep variation. Indeed, previous work with olive baboons (*Papio anubis*) found that individuals slept less when sharing their sleeping tree with more groupmates.[4] We therefore predict that any factor that alters spatial patterns of rest at night could influence sleep outcomes. For example, infants and juveniles (for which we lack behavioral data because they were uncollared) will be additional important sources of disturbance. We also observed the highest synchrony in nighttime activity between M1 (alpha male) and F2 (second-ranked female) (Figure 2D). This is likely because F2 was cyclic and ovulated during the study period (Fürtbauer, unpublished), leading to close physical proximity with M1, as shown in our daytime proximity data.

Future work should now explore the various ecological and social factors (including, but not limited to, dominance hierarchies) that may influence spatial patterns of rest and, in turn, mediate social disruption. Our data suggest that dominant individuals may experience sleep costs due to their social integration; however, they might also gain benefits. For animals sleeping in the open, dominant individuals are predicted to compete for central positions[17] because they may confer lower predation risk,[32–34] thermal benefits,[35] or decrease vulnerability to insect bites.[36] Even if dominants do not compete for central positions, they may "end up" at the center of sleeping aggregations because they have many and strong social bonds[16,37] and, as a result, spatial and social processes are intertwined.[38,39] Further work should now focus on extending and testing the mechanisms we have proposed in baboons and other social sleeping species with strong dominance hierarchies.

We show that dominant baboons experience more interrupted and less rest at night than subordinates, and so social rank may result in unequal sleep-related costs and benefits. Reduced and interrupted sleep can influence various physiological and cognitive functions,[1,2] impacting health and fitness.[3] For example, disrupted sleep can impair decision-making,[40] weaken immune function,[41] and even result in death.[42] However, other evidence suggests that wild animals can drastically reduce sleep for extended periods without obvious costs.[43,44] Whether more dominant baboons in fact incur costs because of "social sleep disruption" remains to be tested. Future work can now do this by, for example, linking variation in sleep persistence and quantity to other behavioral and physiological measures.[19,45–47] Dominant individuals may actually require less sleep because of some other correlated trait,[31,48] or individuals may not be sleep limited, making differences in loss or disruption of sleep across individuals negligible.

Finally, the high levels of nighttime rest synchrony we have found suggest that individuals may not be taking turns at resting to be alert to external dangers as predicted by the "sentinel hypothesis."[49,50] Nighttime leopard attacks are one of the main causes of death for baboons,[51] but given that our study was conducted in a predator-free region of South Africa, it is not known whether the baboon troop's behavior would change under genuine predation threat. However, because active dominant baboons are more likely to interrupt others' rest, more dominant baboons could behave as "indirect" sentinels. In fact, aggregation patterns of sleepers could be fine-tuned to propagate information and thus successfully identify risks but minimize disruption, as seen in other groups with specific social interaction stengths[52–54]; testing this idea would be another interesting direction for future work.

For the first time, we show that social hierarchies impact nighttime rest dynamics in a wild social animal, suggesting possible consequences for sleep. Higher-ranked baboons, which are more connected in spatial networks, exert greater influence on each other's nighttime behavior compared with lower-ranked individuals, resulting in more interrupted and less rest. Given that higher dominance in social animals is linked to better health[55,56] and longer lifespans,[57,58] future work must now investigate whether and how dominance status may impose costs as a consequence of "bad" sleep.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to, and will be fulfilled by, Marco Fele (2252927@swansea.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- csv data have been deposited at Dryad as DOI: https://doi.org/10.5061/dryad.0rxwdbsc9 and are publicly available as of the date of publication.
- All original code has been deposited at GitHub and is publicly available at https://github.com/MarcoFele98 as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

M.F. was funded by an Engineering and Physical Sciences Research Council studentship (project reference: 2252927). M.J.O. was supported by NRF incentive funding. A.M.B. and C.C. were supported by College of Science/Swansea University PhD scholarships. M.P. and A.J.K. were supported by an Office for Naval Research (ONR) Global Grant awarded to A.J.K. (number: N629092112030). We thank the Baboon Technical Team, Cape Nature, and SANParks for permission to conduct our field research. We also thank Human Wildlife Solutions; field assistants Lucy Robertson, Charlotte Solman, and Francesca Marshall-Stochmal; vets Dorothy Breed and Gary Buhrman; and Esme Beamish and Layla King for their help and support. We thank Lucia Pedrazzi and Gui Araujo for their helpful discussions and the South African Environmental Observation Network for providing weather data.

AUTHOR CONTRIBUTIONS

M.F., I.F., and A.J.K. conceptualized the work. Project administration in South Africa was provided by M.J.O'R., and A.M.B. and C.C. collected and curated the data. M.F. conducted the formal analyses, with input from M.P., M.L., I.F., and A.J.K. M.F. produced visualizations, with input from all authors. M.F. was supervised by I.F., M.L., and A.J.K. The original draft was written by M.F., I.F., M.L., M.P., and A.J.K., and all authors were involved in reviewing and editing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - Daytime spatial networks and dominance rank
  - Nighttime data
  - Nighttime rest
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Nighttime rest synchrony
  - Full model specification
  - Calculating rest probability and its confidence interval
  - Nighttime rest quantity, persistence, and restlessness
  - Validation of Markov chain model
  - Social disruption of nighttime rest
  - The consequences of social structure on nighttime rest

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.10.028.

Received: May 9, 2025
Revised: July 31, 2025
Accepted: October 9, 2025
Published: December 12, 2025

REFERENCES

1. Xie, L., Kang, H., Xu, Q., Chen, M.J., Liao, Y., Thiyagarajan, M., O'Donnell, J., Christensen, D.J., Nicholson, C., Iliff, J.J., et al. (2013). Sleep Drives Metabolite Clearance from the Adult Brain. Science *342*, 373–377. https://doi.org/10.1126/science.1241224.
2. Klinzing, J.G., Niethard, N., and Born, J. (2019). Mechanisms of systems memory consolidation during sleep. Nat. Neurosci. *22*, 1598–1610. https://doi.org/10.1038/s41593-019-0467-3.
3. Rechtschaffen, A. (1998). Current Perspectives on the Function of Sleep. Perspect. Biol. Med. *41*, 359–390. https://doi.org/10.1353/pbm.1998.0051.

4. Loftus, J.C., Harel, R., Núñez, C.L., and Crofoot, M.C. (2022). Ecological and social pressures interfere with homeostatic sleep regulation in the wild. eLife *11*, e73695. https://doi.org/10.7554/eLife.73695.
5. Loftus, J.C., Harel, R., Ashbury, A.M., Núñez, C.L., Omondi, G.P., Muttinda, M., Matsumoto-Oda, A., Isbell, L.A., and Crofoot, M.C. (2024). Sharing sleeping sites disrupts sleep but catalyses social tolerance and coordination between groups. Proc. Biol. Sci. *291*, 20241330. https://doi.org/10.1098/rspb.2024.1330.
6. King, A.J., Fehlmann, G., Biro, D., Ward, A.J., and Fürtbauer, I. (2018). Re-wilding Collective Behaviour: An Ecological Perspective. Trends Ecol. Evol. *33*, 347–357. https://doi.org/10.1016/j.tree.2018.03.004.
7. Reinhardt, K.D. (2020). Wild primate sleep: understanding sleep in an ecological context. Curr. Opin. Physiol. *15*, 238–244. https://doi.org/10.1016/j.cophys.2020.04.002.
8. Rattenborg, N.C., de la Iglesia, H.O., Kempenaers, B., Lesku, J.A., Meerlo, P., and Scriba, M.F. (2017). Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. Philos. Trans. R. Soc. Lond. B Biol. Sci. *372*, 20160251. https://doi.org/10.1098/rstb.2016.0251.
9. Samson, D.R., Crittenden, A.N., Mabulla, I.A., Mabulla, A.Z.P., and Nunn, C.L. (2017). Chronotype variation drives night-time sentinel-like behaviour in hunter–gatherers. Proc. Biol. Sci. *284*, 20170967. https://doi.org/10.1098/rspb.2017.0967.
10. Crittenden, A.N., Samson, D.R., Herlosky, K.N., Mabulla, I.A., Mabulla, A.Z.P., and McKenna, J.J. (2018). Infant co-sleeping patterns and maternal sleep quality among Hadza hunter-gatherers. Sleep Health *4*, 527–534. https://doi.org/10.1016/j.sleh.2018.10.005.
11. Mochida, K., and Nishikawa, M. (2014). Sleep duration is affected by social relationships among sleeping partners in wild Japanese macaques. Behav. Processes *103*, 102–104. https://doi.org/10.1016/j.beproc.2013.10.010.
12. Leinonen, L., and Stenberg, D. (1986). Sleep in *Macaca arctoides* and the effects of prazosin. Physiol. Behav. *37*, 199–202. https://doi.org/10.1016/0031-9384(86)90221-0.
13. Crofts, H.S., Wilson, S., Muggleton, N.G., Nutt, D.J., Scott, E.A.M., and Pearce, P.C. (2001). Investigation of the sleep electrocorticogram of the common marmoset (*Callithrix jacchus*) using radiotelemetry. Clin. Neurophysiol. *112*, 2265–2273. https://doi.org/10.1016/S1388-2457(01)00699-X.
14. Mortlock, E., Silovský, V., Güldenpfennig, J., Faltusová, M., Olejarz, A., Börger, L., Ježek, M., Jennings, D.J., and Capellini, I. (2024). Sleep in the wild: the importance of individual effects and environmental conditions on sleep behaviour in wild boar. Proc. Biol. Sci. *291*, 20232115. https://doi.org/10.1098/rspb.2023.2115.
15. De Moor, D.D., and Brent, L.J.N. (2025). Quality, quantity, and the adaptive function of social relationships. Trends Ecol. Evol. S0169-5347(25)00250-2. https://doi.org/10.1016/j.tree.2025.09.004.
16. Fele, M., Fürtbauer, I., Lurgi, M., Papadopoulou, M., Bracken, A.M., Christensen, C., O'Riain, M.J., and King, A.J. (2025). Baboon travel progressions as a 'social spandrel' in collective animal behaviour. Behavioral Ecology, araf022. Behav. Ecol. *36*, araf022. https://doi.org/10.1093/beheco/araf022.
17. Smeltzer, E.A., Stead, S.M., Li, M.F., Samson, D., Kumpan, L.T., and Teichroeb, J.A. (2022). Social sleepers: The effects of social status on sleep in terrestrial mammals. Horm. Behav. *143*, 105181. https://doi.org/10.1016/j.yhbeh.2022.105181.
18. Nagy, M., Ákos, Z., Biro, D., and Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. Nature *464*, 890–893. https://doi.org/10.1038/nature08891.
19. Fürtbauer, I., Christensen, C., Bracken, A., O'Riain, M.J., Heistermann, M., and King, A.J. (2020). Energetics at the urban edge: Environmental and individual predictors of urinary C-peptide levels in wild chacma baboons (*Papio ursinus*). Horm. Behav. *126*, 104846. https://doi.org/10.1016/j.yhbeh.2020.104846.
20. Georgopoulou, D.G., King, A.J., Brown, R.M., and Fürtbauer, I. (2022). Emergence and repeatability of leadership and coordinated motion in fish shoals. Behav. Ecol. *33*, 47–54. https://doi.org/10.1093/beheco/arab108.
21. Davenport, E.C., and El-Sanhurry, N.A. (1991). Phi/Phimax: Review and Synthesis. Educ. Psychol. Meas. *51*, 821–828. https://doi.org/10.1177/001316449105100403.
22. Brividoro, M.V., Oklander, L.I., Cantarelli, V.I., Ponzio, M.F., Ferrari, H.R., and Kowalewski, M.M. (2021). The Effects of Social Factors and Kinship on Co-sleeping of Black-and-Gold Howler Monkeys (Alouatta caraya). Int. J. Primatol. *42*, 876–895. https://doi.org/10.1007/s10764-021-00246-y.
23. Radespiel, U., Cepok, S., Zietemann, V., and Zimmermann, E. (1998). Sex-specific usage patterns of sleeping sites in grey mouse lemurs (Microcebus murinus) in northwestern Madagascar. Am. J. Primatol. *46*, 77–84. https://doi.org/10.1002/(SICI)1098-2345(1998)46:1<77::AID-AJP6>3.0.CO;2-S.
24. Lutermann, H., Verburgt, L., and Rendigs, A. (2010). Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. Anim. Behav. *79*, 1211–1219. https://doi.org/10.1016/j.anbehav.2010.02.017.
25. King, A.J., Douglas, C.M.S., Huchard, E., Isaac, N.J.B., and Cowlishaw, G. (2008). Dominance and Affiliation Mediate Despotism in a Social Primate. Curr. Biol. *18*, 1833–1838. https://doi.org/10.1016/j.cub.2008.10.048.
26. King, A.J., Clark, F.E., and Cowlishaw, G. (2011). The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. Am. J. Primatol. *73*, 768–774. https://doi.org/10.1002/ajp.20918.
27. Majolo, B., Lehmann, J., de Bortoli Vizioli, A., and Schino, G. (2012). Fitness-related benefits of dominance in primates. Am. J. Phys. Anthropol. *147*, 652–660. https://doi.org/10.1002/ajpa.22031.
28. Holekamp, K.E., and Strauss, E.D. (2016). Aggression and dominance: an interdisciplinary overview. Curr. Opin. Behav. Sci. *12*, 44–51. https://doi.org/10.1016/j.cobeha.2016.08.005.
29. Bracken, A.M., Christensen, C., O'Riain, M.J., Fürtbauer, I., and King, A.J. (2022). Flexible group cohesion and coordination, but robust leader-follower roles, in a wild social primate using urban space. Proc. Biol. Sci. *289*, 20212141. https://doi.org/10.1098/rspb.2021.2141.
30. Karamihalev, S., Flachskamm, C., Eren, N., Kimura, M., and Chen, A. (2019). Social context and dominance status contribute to sleep patterns and quality in groups of freely-moving mice. Sci. Rep. *9*, 15190. https://doi.org/10.1038/s41598-019-51375-7.
31. Noser, R., Gygax, L., and Tobler, I. (2003). Sleep and social status in captive gelada baboons (*Theropithecus gelada*). Behav. Brain Res. *147*, 9–15. https://doi.org/10.1016/S0166-4328(03)00111-6.
32. Yagi, N., and Hasegawa, E. (2011). Both cooperation and nest position improve larval survival in the sweat bee, Lasioglossum (Evylaeus) baleicum. J. Ethol. *29*, 63–67. https://doi.org/10.1007/s10164-010-0223-3.
33. Picman, J., Pribil, S., and Isabelle, A. (2022) Antipredator Value of Colonial Resting in Yellow-Headed Blackbirds. 119. 461–472. https://doi.org/10.1642/0004-8038(2002)119[0461:AVOCNI]2.0.CO;2
34. Gazagne, E., Goldblatt, C., Nguyễn, V.T., Brotcorne, F., and Hambuckers, A. (2025). Utilizing thermal imaging drones to investigate sleeping site selection in an arboreal primate. Current Zoology. https://doi.org/10.1093/cz/zoae082.
35. Takahashi, H. (1997). Huddling relationships in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. Primates *38*, 57–68. https://doi.org/10.1007/BF02385922.
36. Mooring, M.S., and Hart, B.L. (1992). Animal Grouping for Protection From Parasites: Selfish Herd and Encounter-Dilution Effects. Behav. *123*, 173–193. https://doi.org/10.1163/156853992X00011.
37. Farine, D.R., Strandburg-Peshkin, A., Couzin, I.D., Berger-Wolf, T.Y., and Crofoot, M.C. (2017). Individual variation in local interaction rules can explain emergent patterns of spatial organization in wild baboons. Proc. R. Soc. Lond. B *284*, 25–29. https://doi.org/10.1098/rspb.2016.2243.

38. Webber, Q.M.R., Albery, G.F., Farine, D.R., Pinter-Wollman, N., Sharma, N., Spiegel, O., Vander Wal, E., and Manlove, K. (2023). Behavioural ecology at the spatial–social interface. Biol. Rev. Camb. Philos. Soc. *98*, 868–886. https://doi.org/10.1111/brv.12934.

39. Albery, G.F., Webber, Q.M.R., Farine, D., Picardi, S., Vander Wal, E., and Manlove, K.R. (2024). Expanding theory, methodology and empirical systems at the spatial–social interface. Philos. Trans. R. Soc. Lond. B Biol. Sci. *379*, 20220534. https://doi.org/10.1098/rstb.2022.0534.

40. Wild, C.J., Nichols, E.S., Battista, M.E., Stojanoski, B., and Owen, A.M. (2018). Dissociable effects of self-reported daily sleep duration on high-level cognitive abilities. Sleep *41*, zsy182. https://doi.org/10.1093/sleep/zsy182.

41. Besedovsky, L., Lange, T., and Haack, M. (2019). The Sleep-Immune Crosstalk in Health and Disease. Physiol. Rev. *99*, 1325–1380. https://doi.org/10.1152/physrev.00010.2018.

42. Rechtschaffen, A., Gilliland, M.A., Bergmann, B.M., and Winter, J.B. (1983). Physiological correlates of prolonged sleep deprivation in rats. Science *221*, 182–184. https://doi.org/10.1126/science.6857280.

43. Kendall-Bar, J.M., Williams, T.M., Mukherji, R., Lozano, D.A., Pitman, J.K., Holser, R.R., Keates, T., Beltran, R.S., Robinson, P.W., Crocker, D.E., et al. (2023). Brain activity of diving seals reveals short sleep cycles at depth. Science *380*, 260–265. https://doi.org/10.1126/science.adf0566.

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

45. Meerlo, P., Pragt, B.J., and Daan, S. (1997). Social stress induces high intensity sleep in rats. Neurosci. Lett. *225*, 41–44. https://doi.org/10.1016/s0304-3940(97)00180-8.

46. Christensen, C., Bracken, A.M., Justin O'Riain, M., Heistermann, M., King, A.J., and Fürtbauer, I. (2022). Simultaneous investigation of urinary and faecal glucocorticoid metabolite concentrations reveals short- versus long-term drivers of HPA-axis activity in a wild primate (*Papio ursinus*). Gen. Comp. Endocrinol. *318*, 113985. https://doi.org/10.1016/j.ygcen.2022.113985.

47. Morgan, A., Christensen, C., Bracken, A.M., O'Riain, M.J., King, A.J., and Fürtbauer, I. (2023). Effects of accelerometry-derived physical activity energy expenditure on urinary C-peptide levels in a wild primate (*Papio ursinus*). Horm. Behav. *152*, 105355. https://doi.org/10.1016/j.yhbeh.2023.105355.

48. Shuboni-Mulligan, D.D., Young, D.L., De La Cruz Minyety, J., Vera, E., Munasinghe, J., Gall, A.J., Gilbert, M.R., Armstrong, T.S., and Smart, D.K. (2021). Impact of age on the circadian visual system and the sleep-wake cycle in mus musculus. npj Aging Mech. Dis. *7*, 10. https://doi.org/10.1038/s41514-021-00063-w.

49. Burger, A.L., Fennessy, J., Fennessy, S., and Dierkes, P.W. (2020). Nightly selection of resting sites and group behavior reveal antipredator strategies in giraffe. Ecol. Evol. *10*, 2917–2927. https://doi.org/10.1002/ece3.6106.

50. McKinnon, L., Shattuck, E.C., and Samson, D.R. (2023). Sound reasons for unsound sleep: Comparative support for the sentinel hypothesis in industrial and nonindustrial groups. Evol. Med. Public Health *11*, 53–66. https://doi.org/10.1093/emph/eoac039.

51. Bidner, L.R., Matsumoto-Oda, A., and Isbell, L.A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. Am. J. Primatol. *80*, e22932. https://doi.org/10.1002/ajp.22932.

52. Fahimipour, A.K., Gil, M.A., Celis, M.R., Hein, G.F., Martin, B.T., and Hein, A.M. (2023). Wild animals suppress the spread of socially transmitted misinformation. Proc. Natl. Acad. Sci. USA. *120*, e2215428120. https://doi.org/10.1073/pnas.2215428120.

53. Gómez-Nava, L., Lange, R.T., Klamser, P.P., Lukas, J., Arias-Rodriguez, L., Bierbach, D., Krause, J., Sprekeler, H., and Romanczuk, P. (2023). Fish shoals resemble a stochastic excitable system driven by environmental perturbations. Nat. Phys. *19*, 663–669. https://doi.org/10.1038/s41567-022-01916-1.

54. McCormick, J.S., White, T.E., Middleton, E.J.T., and Latty, T. (2024). Information cascades spread adaptive and maladaptive behaviours in group-living animals. Anim. Behav. *209*, 53–62. https://doi.org/10.1016/j.anbehav.2023.12.007.

55. Sapolsky, R.M. (2004). Social Status and Health in Humans and Other Animals. Annu. Rev. Anthropol. *33*, 393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000.

56. Sapolsky, R.M. (2005). The Influence of Social Hierarchy on Primate Health. Science *308*, 648–652. https://doi.org/10.1126/science.1106477.

57. Campos, F.A., Villavicencio, F., Archie, E.A., Colchero, F., and Alberts, S.C. (2020). Social bonds, social status and survival in wild baboons: a tale of two sexes. Philos. Trans. R. Soc. Lond. B Biol. Sci. *375*, 20190621. https://doi.org/10.1098/rstb.2019.0621.

58. Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., Bartolomucci, A., Yang, Y.C., Aiello, A.E., O'Rand, A., et al. (2020). Social determinants of health and survival in humans and other animals. Science *368*, eaax9553. https://doi.org/10.1126/science.aax9553.

59. Chakravarty, P., Ashbury, A.M., Strandburg-Peshkin, A., Iffelsberger, J., Goldshtein, A., Schuppli, C., Snell, K.R.S., Charpentier, M.J.E., Núñez, C.L., Gaggioni, G., et al. (2024). The sociality of sleep in animal groups. Trends Ecol. Evol. *39*, 1090–1101. https://doi.org/10.1016/j.tree.2024.07.011.

60. Stueckle, S., and Zinner, D. (2008). To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. Anim. Behav. *75*, 1995–2004. https://doi.org/10.1016/j.anbehav.2007.12.012.

61. Kaplan, B.S., O'Riain, M.J., van Eeden, R., and King, A.J. (2011). A Low-Cost Manipulation of Food Resources Reduces Spatial Overlap Between Baboons (Papio ursinus) and Humans in Conflict. Int. J. Primatol. *32*, 1397–1412. https://doi.org/10.1007/s10764-011-9541-8.

62. King, A.J., and Sueur, C. (2011). Where Next? Group Coordination and Collective Decision Making by Primates. Int. J. Primatol. *32*, 1245–1267. https://doi.org/10.1007/s10764-011-9526-7.

63. Sueur, C. (2011). Group decision-making in chacma baboons: leadership, order and communication during movement. BMC Ecol. *11*, 26. https://doi.org/10.1186/1472-6785-11-26.

64. Bracken, A.M., Christensen, C., O'Riain, M.J., Fehlmann, G., Holton, M.D., Hopkins, P.W., Fürtbauer, I., and King, A.J. (2022). Socioecology Explains Individual Variation in Urban Space Use in Response to Management in Cape Chacma Baboons (Papio ursinus). Int. J. Primatol. *43*, 1159–1176. https://doi.org/10.1007/s10764-021-00247-x.

65. Ropert-Coudert, Y., and Wilson, R.P. (2005). Trends and perspectives in animal-attached remote sensing. Front. Ecol. Environ. *3*, 437–444. https://doi.org/10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2.

66. Christensen, C., Bracken, A.M., O'Riain, M.J., Fehlmann, G., Holton, M., Hopkins, P., King, A.J., and Fürtbauer, I. (2023). Quantifying allo-grooming in wild chacma baboons (Papio ursinus) using tri-axial acceleration data and machine learning. R. Soc. Open Sci. *10*, 221103. https://doi.org/10.1098/rsos.221103.

67. Thieurmel, B., and Elmarhraoui, A. (2017) Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. https://doi.org/10.32614/CRAN.package.suncalc.

68. Erkert, H.G., and Kappeler, P.M. (2004). Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (Propithecus v. verreauxi; Primates: Indriidae). Behav. Ecol. Sociobiol. *57*, 174–186. https://doi.org/10.1007/s00265-004-0845-y.

69. Donati, G., Santini, L., Razafindramanana, J., Boitani, L., and Borgognini-Tarli, S. (2013). (Un-)expected nocturnal activity in "Diurnal" Lemur catta supports cathemerality as one of the key adaptations of the lemurid radiation. Am. J. Phys. Anthropol. *150*, 99–106. https://doi.org/10.1002/ajpa.22180.

70. Svensson, M.S., Nekaris, K.a. i., Bearder, S.K., Bettridge, C.M., Butynski, T.M., Cheyne, S.M., Das, N., de Jong, Y.A., Luhrs, A.M., Luncz, L.V., et al. (2018). Sleep patterns, daytime predation, and the evolution of diurnal sleep site selection in lorisiforms. American Journal of Physical Anthropology *166*, 563–577. https://doi.org/10.1002/ajpa.23450.

71. Kim, J.W., Lee, J.S., Robinson, P.A., and Jeong, D.U. (2009). Markov Analysis of Sleep Dynamics. Phys. Rev. Lett. *102*, 178104. https://doi.org/10.1103/PhysRevLett.102.178104.

72. Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., Skaug, H., Nielsen, A., Berg, C., and Van Bentham, K. (2017) glmmTMB: Generalized Linear Mixed Models Using Template Model Builder. https://doi.org/10.32614/CRAN.package.glmmTMB.

73. Dean, R.T., and Dunsmuir, W.T.M. (2016). Dangers and uses of cross-correlation in analyzing time series in perception, performance, movement, and neuroscience: The importance of constructing transfer function autoregressive models. Behav. Res. Methods *48*, 783–802. https://doi.org/10.3758/s13428-015-0611-2.

74. Hart, J.D.A., Weiss, M.N., Franks, D.W., and Brent, L.J.N. (2023). BISoN: A Bayesian framework for inference of social networks. Methods Ecol. Evol. *14*, 2411–2420. https://doi.org/10.1111/2041-210X.14171.

75. Tranmer, M., Steel, D., and Browne, W.J. (2014). Multiple-Membership Multiple-Classification Models for Social Network and Group Dependences. J. R. Stat. Soc. Ser. A. Stat. Soc. *177*, 439–455. https://doi.org/10.1111/rssa.12021.

76. Stan Development Team. (2024). Stan. Stan user's guide. https://mc-stan.org/docs/.

77. Csárdi, G., Nepusz, T., Traag, V., Horvát, S., Zanini, F., Noom, D., Müller, K., Salmon, M., Antonov, M., and details. C.Z.I. igraph author. (2024) Igraph: Network Analysis and Visualization, [Version 2.0.3].

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data for reproducing all analyses	This paper	https://doi.org/10.5061/dryad.0rxwdbsc9
Experimental models: Organisms/strains		
Chacma baboon (*Papio ursinus*)	wild	N/A
Software and algorithms		
R 4.3.0	R Core Team	https://www.R-project.org/
Code to reproduce results	GitHub	https://github.com/MarcoFele98

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Baboons are an ideal model system in which to explore the potential effect of a group's social structure on sleep.[4,59] Chacma baboon groups comprise a complex social system with a stable linear dominance hierarchy that mediates association patterns, with higher ranked baboons occupying more central positions in social networks.[16,26] Furthermore, higher-ranked individuals are critical to group-level processes during the daytime (e.g. group decision-making and coordination[25,29,60–63]).

We studied the 'Da Gama' baboon troop in Da Gama Park, Cape Town, South Africa (−34.15562° N, 18.39858° E) with permission from Cape Nature, permit number: CN44-59-6527 and SANparks, permit number: CRC/2018-2019/008-2018/V1. The troop consisted of approximately 50 individuals (2 adult males and 19 adult females). Baboon groups on the Cape Peninsula range near to and within urban areas of the City of Cape Town and our study troop home range was predominantly in Table Mountain National Park and included 13% of a residential suburb of Da Gama Park.[64] This troop was selected for logistical reasons: its home range was readily accessible for regular monitoring and data collection, and the group was sufficiently large to provide data on many individuals, allowing investigation of social dynamics.

Most adults in the study troop (16/22) were fitted with our bespoke tracking collars[46,64] approved by Swansea University's Ethics Committee (IP-1315-5). Collars contained tri-axial accelerometer, Daily Diary,[65] recording at 40 Hz for 24hrs a day, and GPS tags (GiPSy 5 tags, TechnoSmArt, Italy) recording baboon position between 08.00h and 20.00h local time (UTC+2) at 1Hz. GPS positional accuracy was within 5m (and often much less than this) and erroneous fixes (average of 0.01% of GPS points per collar) were removed and interpolated, as described in Bracken et al.[64] Because of collar failures, we have full accelerometery data for 12 individuals (2/2 males, 10/19 females) for 25 continuous astronomical nights between 2nd August 2018 and 27th of August 2018, and daytime GPS continuously between 30/7/2018 and 15/9/2018 for 13 individuals (2/2 males, 11/19 females) (Table S2). Combined accelerometer and GPS data are therefore available for 9 individuals (2/2 males, 7/19 females). Previous work suggests no individual level biases in activity patterns because of how the tracking collar was mounted.[47,66]

METHOD DETAILS

Daytime spatial networks and dominance rank

We constructed a network of inter-individual distances (or pairwise spatial associations) using our GPS data. We represent every individual as a node, and each edge is the median pairwise individual distance. We use median pairwise distances for our network edges because we have complete data for collared individuals, with no need to control for sampling effort. Behavioural data on dominance interactions was collected *ad libitum* during direct observation over 78 days.[29,64] Dominance rank was determined based on the outcome of directly observed dyadic agonistic interactions and then standardised between 0 (lowest) and 1 (highest) and full details of dominance analyses are provided in Fürtbauer et al.[19]

Nighttime data

During the period for which we have full night-time data (see above), the troop slept on one or multiple roofs of an apartment block or in large trees in the urban space except for three nights when they slept in natural space. Activity was comparable in all qualitative comparisons we made between the natural and urban sleep sites. Direct observations indicate that baboons were not always at rest in the same location at sunset, e.g., in different trees, but we cannot determine exact night-time locations because our GPS did not collect data at night. This means that two individuals may have slept far enough apart to have little or no interaction overnight. Crucially, this lack of interaction is what our analyses are designed to detect: we quantify influence based on observable patterns of synchrony or independence in their activity (see sections on 'Night-time Rest synchrony' and 'Social disruption of night-time rest', below).

Nighttime rest

Astronomical night is defined as when the geometric centre of the sun is 18 degrees below the horizon, occurring approximately between ~20:00 and ~06:00 in our study system. We obtained this data with the R package "suncalc"[67]. We are not able to use electrophysiology to study baboon sleep in the wild. Because baboons assume a specific posture and remain immobile when sleeping[8] we use accelerometer data was used as a proxy for sleep.[4] For every second in our accelerometer data, we calculate the average vector of dynamic body acceleration (VeDBA) (for details see Christensen et al.[66]) and consider an individual at complete rest when mean VeDBA are below 0.04, and active otherwise. VeDBA this low is well within the range of rest behaviour previously validated by comparing accelerometers output and video footage.[66] This definition allows us to study state on a second-by-second basis, rather than averaging or summing activity over some period as a proxy for sleep[68] and this method is likely more accurate in identifying rest than behavioural classification from direct observation or video.[31,69,70] We also conducted sensitivity analyses for our definition of rest (with threshold 0.03 and 0.05 for VeDBA) which suggest that our results are robust to different thresholding values (Tables S1).

QUANTIFICATION AND STATISTICAL ANALYSIS

Nighttime rest synchrony

To investigate group level rest synchrony, we compared the observed distribution of the probability of finding n individuals simultaneously resting with a null distribution in which individuals behave independently of each other. To calculate this, we first found for every individual i the observed probability of resting $p_{i,R}$ as the total proportion of time spent resting. We then calculated the probability of a unique combination of resting and active individuals by multiplying together the probabilities of resting $p_{i,R}$ for the resting individuals with the probabilities of being active $1 - p_{i,R}$ for the active individuals. We find the null probability of n individuals resting by summing all the probabilities of having a group combination where n individuals are resting. We used a similar approach to investigate rest synchrony between pairs of individuals. We defined the null expectation of pairwise synchrony for individual i and j as $p_{i,R}p_{j,R} + \left(1 - p_{i,R}\right)\left(1 - p_{j,R}\right)$, which is the probability both are resting plus the probability both are active in case they behaved independently. We quantified the observed pairwise synchrony by calculating the proportion of time two individuals are in the same state in the data and divide this with the null expectation. This metric therefore provides information on how likely it is for two individuals to be in the same state, compared to what we would expect if their behaviour was independent.

Full model specification

$$state_{t+1} \sim bernoulli(p_{R\to R}|state_t = 1)$$

$$state_{t+1} \sim bernoulli(1 - p_{A\to A}|state_t = 0)$$

$$\text{with } p : p_{R\to R}, p_{A\to A}$$

$$logit(p) = (1|\text{id}) + \text{rest\_previous\_night} + \text{dominance} * \big(\text{number\_resting} +$$

$$\text{avg\_dominance\_resting}\big) +$$

$$\text{night\_duration} + (1|\text{night}) + \text{mean\_temperature} + \text{precipitation} + \text{moon\_fraction}$$

Complete specification of Markov chain model. Each parameter is estimated through a logistic regression, considering individual characteristics, social environment, and control covariates. State = 1 corresponds to resting, state = 0 corresponds to active.

Calculating rest probability and its confidence interval

Given the Markov chain model described in the main text, we have a transition matrix $\boldsymbol{M}$ which for convenience we parametrize here by considering the transition probabilities between states $p_{R\to A}$ and $p_{A\to R}$ as the free parameters estimated by the logistic regression models.

To find the rest probability p_R, which is not free but derived directly from the two transition parameters, we start by consider $\boldsymbol{v_t}$ the column vector of size 2 which defines the probability of rest (first entry) or active (second entry) at time t. We can find $\boldsymbol{v_t}$ by repeatedly multiplying the transition matrix $\boldsymbol{M}$ with the initial probabilities $\boldsymbol{v_0}$ so that $\boldsymbol{v_t} = \boldsymbol{M}^t\, \boldsymbol{v_0}$. We can find the steady state, i.e., the state probabilities that do not change between timesteps, by solving $\boldsymbol{v_{t+1}} = \boldsymbol{M}\boldsymbol{v_t}$. More explicitly, we find the probability of rest p_R that solves the system of equations given by the dot product:

$$\begin{pmatrix} p_R \\ 1 - p_R \end{pmatrix} = \begin{pmatrix} 1 - p_{R\to A} & p_{A\to R} \\ p_{R\to A} & 1 - p_{A\to R} \end{pmatrix} \begin{pmatrix} p_R \\ 1 - p_R \end{pmatrix}$$

We find $p_R = \frac{p_{A\to R}}{p_{A\to R} + p_{R\to A}}$, which is then converted to the alternative parameterization in the main text ($p_R = \frac{p_{A\to R}}{p_{A\to R} + p_{R\to A}} = \frac{1 - \widehat{p}_{A\to A}}{2 - \widehat{p}_{A\to A} - \widehat{p}_{R\to R}}$, with $1 - \widehat{p}_{A\to A} = p_{A\to R}$ and $1 - \widehat{p}_{R\to R} = p_{R\to A}$).The intuition behind p_R is that the probability of resting is equal to the “push” towards the rest state over the total “push”. The upper bound for the confidence interval of p_R is calculated by substituting $p_{A\to R}$ with $p_{A\to R} + SE(p_{A\to R})$ and $p_{R\to A}$ with $p_{R\to A} - SE(p_{R\to A})$, where SE($p$) is the standard error of the parameter estimated from the logistic regression. The +/- signs are inverted to find the lower bound. The intuitive reasoning is that the highest estimate for transitioning to rest and the lowest estimate for leaving rest will lead to the highest estimate of being in a rest state overall.

Nighttime rest quantity, persistence, and restlessness

We predicted (indicated by $\hat{}$): (i) rest quantity, $\hat{p}_R$ (the overall probability of resting during the night), using (ii) rest persistence, $\hat{p}_{R\to R}$ (i.e., the probability of resting in successive timesteps), and (iii) restlessness, $\hat{p}_{A\to A}$, (i.e., the probability of being active in successive timesteps). We did this by considering the time series of “resting” and “active” states of each individual as an inhomogeneous Markov chain (Figure 1C).[71] “Inhomogeneous” refers to the state transition probabilities changing depending on social and environmental variables that vary in time (described below). To find the rest probability $\hat{p}_R$, we calculated $\hat{p}_R = \frac{1-\hat{p}_{A\to A}}{2-\hat{p}_{A\to A}-\hat{p}_{R\to R}}$, assuming the Markov chain has reached steady state. To find the predicted transition probabilities $\hat{p}_{S\to S}$ and $\hat{p}_{A\to A}$ of the Markov chain, depending on the current state s_t at time t, we fitted two logistic regression models using the R package glmTMB.[72] Specifically, we fitted one logistic regression for when an individual is resting, and one when it is active (Figure 1B). The response variable for both logistic regressions is whether an individual is resting (1) or active (0) in the next time step s_{t+1}. To control for individual-level effects (non-independence of sleep on successive nights), we included the observed rest probability during the previous night as a continuous variable and individual identity and night number as a random effect. To test how dominance impacts sleep, we included standardised dominance rank as a continuous variable. To test whether the state of other individuals changes the probability of transitioning to resting or active, we added the number of resting group members as an explanatory variable. We also included the average dominance of the resting individuals in interaction with individual dominance, to test if an individual is more or less likely to transition when the resting individuals are on average of higher, lower, or similar dominance. We also included environmental factors as controls (Figure 1B). We fitted rain conditions (rainfall yes or no; because sleep may be disturbed or activity reduced when it rains), the average temperature (°C; because activity may be reduced on colder nights), moon illumination (fraction of the moon that is visible; because activity may increase on brighter nights), night duration (seconds; because baboons may sleep proportionally less on longer nights). We gathered weather and temperature data at one hour resolution from the Cape Town weather stations of the South African Weather Service. We obtained moon illumination with the R package “suncalc”[67], with one indicating full moon and zero indicating new moon.

Validation of Markov chain model

The Markov chain model does not capture every aspect of nighttime rest (Figure S3). For example, we cannot model the long tails of the frequency distribution of duration of bouts of continuous behaviour because our Markov chain model results in an exponential distribution for behavioural duration, underrepresenting long bouts of continuous behaviour, which nevertheless are *very rare* (around 10 per individual over 25 nights). Rare events can be very important for some research questions, but because they are rare (frequency of ~ten events per individual in our study period of ~25 nights) they do not bias our estimation of our model parameters much. This is because a “well timed” one second interruption of a rare and long behavioural bout will drastically change the duration of the bout but will barely impact transition probabilities. This could be avoided by using a semi-Markov process, where the time spent in state is included as covariate predicting the state transition probabilities, but is not necessary to understand the patterns of rest we investigated here and is outside the scope of our project.

In our model, we assume the Markov chain has reached steady state and acknowledge some bias in estimating durations of active and inactive states (does not capture rare long continuous bouts of rest or activity: Figures S3). To assess whether this affects our findings and the accuracy of state duration estimates, for each explanatory variable, we calculated the average observed resting time and compared it to the model’s prediction. Our model predicts resting time within an error margin of ±0.0015 proportionally, equivalent to ±0.6 hours over 203 total rest hours across 25 days.

Social disruption of nighttime rest

We performed a cross-correlation analysis[18–20] of the behavioural time series for each pair of individuals state at different temporal shifts. To do so, we temporally shifted the start of every focal individual’s timeseries and found the pairwise cross correlation with every other individual’s time series for different time lags (considering shifts spanning from -250 seconds to shift +250 seconds, see S1). The correlation coefficient for a binomial timeseries is ψ/ψ_{max},[21] where ψ is the covariance between the timeseries and ψ_{max} is the maximum possible covariance. A peak in the cross correlation indicates the time lag for which the behaviour of the focal individual preferentially predicts the behaviour of the other. If the peak is positive, the focal individual is a “leader” and influences the other. If the peak is negative, the focal individual is a “follower” and is influenced by the other. Temporal autocorrelation of the timeseries (which is accounted in the previous model by using a Markov chain) does not bias the calculation of the cross correlation coefficient ψ/ψ_{max}.[73]

We constructed an influence network for sleep disruption across our dataset, where every individual is represented as a node, and directed edges go from the influencer to the influenced individuals, with an edge value equal to the peak cross correlation. To test whether dominance predicts influence, we performed nodal regression[74] by calculating the proportion of interactions in which the focal individual influences others (was a leader, see above). We then fitted a logistic regression with individual dominance and sex as predictors, and the proportion of influenced individuals as response. To test whether the effect of dominance is significantly bigger than zero, we created a null distribution for the dominance effect by calculating it on a randomized network where we shuffle the edges across pairs of individuals (5000 times). We tested whether the observed effect is higher than the effect associated with the highest 0.05 of this null distribution. To investigate whether dominance is associated with higher influence strength, we performed dyadic regression[74,75] linear mixed model with peak cross-correlations as response, and individual dominance as predictor. We controlled for individual identity as a random effect. As fixed effects we included the sex of the individual and sex composition of the pair (male-male, male-female, female-female). To control for data dependencies by including individual identity in all our dyadic regressions, we use STAN and rstan for all models.[76] We ensured MCMC convergence by visually inspecting the chain and ensuring r-hat values were close to one.

The consequences of social structure on nighttime rest

To test if closely ranked baboons are closer in space, we performed dyadic regression[74,75] by fitting a linear mixed model with pairwise median inter-individual distance as the response variable, individual dominance as the explanatory variable (standardized), individual identity as a random effect, and pair sex composition (male-male, male-female, female-female) as a control covariate. We investigated whether individuals that spend more time closer during the day influence each other's behaviour more strongly during the night by performing dyadic regression where the log cross-correlation peak ψ/ψ_{max} was the response, log daytime spatial proximity (standardized) was the explanatory variable, individual identity as a random effect, and individual and pair sex composition (male-male, male-female, female-female) as a control covariate. Lastly, we investigated how dominance may impact network centrality and thus social sleep disruption. To do this, we fitted two linear mixed models with centrality in the influence network and in the spatial proximity network, respectively, as response variables, individual dominance, and sex as predictor, and individual identity as random factor. We used eigenvector centrality as our network centrality metric, which assigns a high score to individuals connected to individuals that are also well connected to others.[77] Eigen vector centrality c_i for individual i is the i^{th} entry of the left eigenvector associated with the leading eigenvalue of the adjacency matrix of the network.