# High-resolution tracking of social interactions highlights nocturnal drivers of animal sociality

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## Abstract

Network structure is a key driver of animal survival, reproductive success, pathogen transmission, and information spread in animal societies. Yet our knowledge of animal social structure is mostly limited to species' main activity periods. Here, we investigated the role of nocturnal sociality in a wild herbivore population, the rock hyrax (Procavia capensis). Using proximity loggers, we recorded nearly 15,000 encounters over 27 days. We show that hyraxes are choosier regarding their social partners at night. At multiple temporal scales, they maintain their overall network topology while reallocating the weights of social relationships. Our results show that nighttime underground sociality can be an optimal baseline shaping hyrax diurnal interactions above ground. The results also suggest that complex social dynamics are not reserved to species characterized by high cognitive abilities and shed light on the function of nocturnal social interactions in diurnal social species.

# High-resolution tracking of social interactions highlights nocturnal drivers of animal sociality

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## Statement of authorship:

CB, RB, and YG collected the data. CB and AI designed the study. CB designed and performed the analysis. CB wrote the manuscript. AI and LK provided guidance. All authors participated in the revision of the manuscript.

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https://github.com/camillebordes/Hyrax_daily_SND

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# Abstract

Network structure is a key driver of animal survival, reproductive success, pathogen transmission, and information spread in animal societies. Yet our knowledge of animal social structure is mostly limited to species' main activity periods. Here, we investigated the role of nocturnal sociality in a wild herbivore population, the rock hyrax (*Procavia capensis*). Using proximity loggers, we recorded nearly 15,000 encounters over 27 days. We show that hyraxes are choosier regarding their social partners at night. At multiple temporal scales, they maintain their overall network topology while reallocating the weights of social relationships. Our results show that nighttime underground sociality can be an optimal baseline shaping hyrax diurnal interactions above ground. The results also suggest that complex social dynamics are not reserved to species characterized by high cognitive abilities and shed light on the function of nocturnal social interactions in diurnal social species.

# Introduction

Because animals are highly vulnerable when asleep (Siegel 2008), they must find appropriate sleeping sites to protect themselves from predators (Lima *et al.* 2005), implying that sleeping strategies and related behaviors are adaptive (Tougeron & Abram 2017; Lesku *et al.* 2019). Social sleeping increases the chances to detect predators, helps mitigate low temperatures, and improves sleep quality. For instance, social sleepers naturally synchronize their sleep (Karamihalev *et al.* 2019) and spend more time in deep sleep stages than solitary individuals, which results in shorter total sleeping time (Capellini *et al.* 2008), and shorter exposure to predators.

Sleeping in groups also exposes individuals to intra-specific aggression, but it is a lesser risk than being predated while asleep. Hence, most diurnal social species maintain sociality at night to limit predation risk (Lima *et al.* 2005) despite the cost of social stress. Several species of apes form larger social groups at night than during the day (Ogawa *et al.* 2007; Mulavwa *et al.* 2010) and become more tolerant of conspecifics' proximity when sleeping in dangerous habitats (Kummer & Kurt 1963; Matsuda *et al.* 2010; Schreier & Swedell 2012). When the risk of predation is higher than the risk of intra-specific aggression at night, sleeping groups become larger, denser, and less selective (Ogawa & Takahashi 2002). Conversely, when the risk of predation becomes negligible compared to the risk of being attacked by a conspecific, daytime groups either split into sub-units, sometimes leading individuals to sleep alone (Snyder-Mackler *et al.* 2012), or adapt their sleeping phases. For example, unfamiliar macaques synchronize their wakefulness more than individuals coming from the same natal group (Mochida & Nishikawa 2014), which reduces the risk of intraspecific aggression from unfamiliar individuals.

These two factors are further mitigated by the need for efficient thermoregulation when asleep, as well as the accessibility of sleeping sites. Indeed, the size of nighttime aggregations is limited by sleeping site availability and results in intra-specific competition for the most valuable positions (Di Bitetti *et al.* 2000). In habitats where shelters are a limiting resource, animal societies have developed fission-fusion dynamics where large foraging aggregations split into smaller sleeping units to accommodate limited shelter space (Snyder-Mackler *et al.* 2012). Under challenging thermal conditions, however, sleeping aggregations become larger to maintain body temperature (Takahashi 1997), promoting less selective social bonds. This suggests that the choice of sleeping partners around sleeping periods has important fitness consequences.

Despite the importance of nighttime ecology (Park *et al.* 1940; Gaston 2019), little attention has been given to animal sociality outside their main activity periods. For decades, data related to animal sociality have been collected via direct behavioural observations, which are spatially and temporally constrained by observers' abilities. Consequently, studies on the sociality of wild animals have mostly been limited to diurnal species (easier to observe) when observations were possible (mainly daytime and in open spaces). The recent revolution of automated data collection has increased the accuracy, resolution, and spatiotemporal range of behavioural data, facilitating the tracking of social interactions around the clock (Krause *et al.* 2013; Börger *et al.* 2020). Yet, few biologging-based studies investigated the structure of animal social networks outside their main activity period (but see Silk *et al.* 2017 and Smith *et al.* 2018). This gap is important to address considering the importance of sleep for individual fitness (Tougeron & Abram 2017).

In this study, we use proximity biologging data and social network analysis to investigate the nighttime sociality of a wild population of rock hyraxes (*Procavia capensis*). Rock hyraxes are medium-sized mammals living in groups of 20 individuals on average. These groups usually include one resident male, several adult females, and their offspring. Hyraxes raise their young collectively, sometimes forming heterospecific groups (Barry & Mundy 2002), and are organized in egalitarian societies (Barocas *et al.* 2011) following the principle of 'structural balance' (Ilany *et al.* 2013).

Mainly active during daytime, they retreat into underground natural cavities at night to protect themselves from predators. As daylight lasts approximately 14 hours in summer at our study site, they can spend up to 10 hours a day underground, although they venture aboveground during moonlit nights (Coe 1961). Laboratory-based studies showed that rock hyraxes sleep on average 6 to 7 hours per day and that their sleep state durations are unaffected by light or dark conditions. Therefore, rock hyraxes are not strictly diurnal but rather have polycyclic sleeping patterns (Gravett *et al.* 2012). Captive animals show longer sleeping periods than their wild conspecifics (Capellini *et al.* 2008) due to lower exposure to stressful environmental conditions (Lesku *et al.* 2019). Thus, wild hyraxes likely are active at night, although no study has yet determined the range of behaviours they express underground. Consequently, they are a good candidate species to explore nighttime sociality and how it relates to daytime social structure.

We tracked the social contacts between 28 wild hyraxes from the Ein Gedi Nature Reserve (Israel) for 27 consecutive days to 1) characterize their social behaviour at night, 2) determine if the nighttime social structure can predict daytime social structure, and 3) describe social changes occurring over crepuscule. Although hyraxes are not strictly diurnal, we expected them to sleep mainly at night, underground. Thus, we should observe more contacts during daytime but longer encounters during nighttime. As hyraxes mainly interact within their social group, with whom they share a common den at night and most of their daytime activities, we expect group composition to remain constant between day and night. Due to negligible predation risk underground, we predict animals will be more selective when foraging during the day.

We show that hyraxes readjust their social interactions before sleeping. They were found less social and consistently more selective of their social partners at night, supporting the idea that potential sleeping partners are carefully chosen. We suggest that nighttime sociality represents an optimum in hyrax social behaviour and may have strong impact on social bonds expressed in other contexts. Our findings shed light on social network dynamics at a very short timescale and strengthen the idea that studying social network structures outside the animals' main period of activity advances our understanding of their ecology.

# Materials and methods

## Data collection and sampling

We conducted fieldwork in the Ein Gedi Nature Reserve in Israel (31° 28′ N, 35° 24′ E) on two distinct study sites located approximately 2.5 km apart. Between March and August 2017, we studied 83 wild rock hyraxes, 37 of which were old enough to receive a biologger. Hyraxes were trapped between March and June according to previously published protocols (Koren *et al.* 2008). Briefly we set 30 live box traps in strategic trapping sites before sunrise for about 4 hours. Any trapped hyrax heavier than 1.8 kg was anaesthetized using 0.1mg/kg of ketamine hydrochloride (intramuscular injection) and fitted with Sirtrack E2C-171-A proximity biologgers. Having assessed loggers' quality under laboratory conditions (Boyland *et al.* 2013) before deployment, we deployed loggers that consistently performed well together, whereas pairs of loggers showing poor performance were deployed in different study sites to minimize their chances of encounter.

Out of the eligible population, we successfully equipped 28 individuals with biologgers between June and August 2017. We later only retained a period when the study population remained stable (27 consecutive days, see *Supporting Information*). Hyraxes were trapped again at the end of the field season to retrieve their collars. Notably, 7 proximity loggers were either never retrieved, or permanently damaged, resulting in the loss of the data they recorded.

## Social network analysis

### Constructing proximity-based networks

Due to inter- and intra-logger variability (Drewe *et al.* 2012), proximity data require multiple corrections to obtain reliable lists of social interactions (see *Supporting information*).

Two proximity loggers normally store duplicated records of their encounter in their internal memory. But. as some loggers were never retrieved, the social behaviour of these individuals was only recorded by other devices. To correct for missing collars, we removed duplicate proximity contacts from dyads where both collars were retrieved by randomly excluding the records from one of the loggers (see Silk *et al.* 2017). We then repeated the data analysis multiple times to ensure that our results were qualitatively robust to the subset of loggers retained by this random selection.

As part of raw data pre-processing, we divided the study period into intervals of five minutes for which each dyad received a value of either 0 (no interaction during the interval) or 1 (the dyad did interact during the interval). A 5- minutes interval when a dyad is found interacting is considered a ‘proximity event’. After pre-processing, the dataset consisted of 15,047 proximity events. When constructing a network, we define the strength of interaction for a pair of individuals as the number of shared proximity events out of the number of proximity events either animal shared with any other individual (Hoppitt & Farine 2018).

### Calculating network traits

Community structure is a crucial feature of social network analysis. We used the Overlapping Cluster Detection algorithm from the '*linkcomm*' R package (Kalinka & Tomancak 2011) to detect nested overlapping communities in the study population (Figure 1). As some individuals interact with multiple groups every day, they can be affiliated to several communities at the same time. We defined their group as the union of all their communities. Preliminary exploration of proximity data revealed that 7 proximity events (0.04%) occurred between the assigned groups. We calculated 5 node-level and 2 group-level network traits (Table 1) using the '*igraph*' R package (Csardi & Nepusz 2006). We also calculated the standard deviation of 3 individual network traits within groups (i.e., degree centrality, eigenvector centrality, and individual selectivity).

## Data analysis

### Discriminating between 'passive' and 'active' sociality at night

Sleep is associated with lower levels of awareness (Siegel 2008), which affects individuals' likelihood to initiate interactions or end existing ones. When two awake individuals are engaged in a long interaction, they may break the ongoing encounter at any moment. But once animals are asleep, the contact lasts as long as both individuals remain unconscious. Consequently, social encounters recorded when two individuals are asleep are not the result of a repeated and active choice to remain near each other ('active' contacts). Rather, they are the result of a social behaviour expressed while awake and being carried out after losing consciousness ('passive' contacts). Due to their length, ‘passive’ contacts strongly affect the social structure of an aggregated network, which may mask the ‘active’ sociality expressed in-between sleeping bouts. Since nighttime social structure is predominantly sleep-related in rock hyraxes, comparing social behaviours between daytime and nighttime requires ignoring sleeping associations. We analyzed the correlation between networks based on interactions of different lengths to identify ‘passive’ associations. Our results showed that a threshold of 25 minutes in interaction length accurately discriminates between two different social structures, prompting us to divide contacts into ‘passive’ (>25 minutes) and ‘active’ (<25 minutes) in the rest of this study (*Supporting information)*.

### Social structure across phases of the day and social contexts

We divided daytime and nighttime networks into ‘passive’ and ‘active’ sub-networks and compared them using the cosine similarity index implemented in the ‘*lsa*’ R Package (Wild 2020). Considering the fundamental differences in behavioural states and social contexts when animals are resting compared to when they are active, we expected nighttime ‘passive’ networks to be relatively poor predictors of any other type of network. As group members synchronize their activities throughout the day, we expected hyraxes to rest with individuals sharing their activities; thus, ‘active’ and ‘passive’ daytime networks should be correlated. In addition, because ecological conditions are different between daytime and nighttime, we did not expect ‘active’ daytime networks to accurately predict ‘active’ nighttime networks.

### Comparing ‘active’ social networks across days

We divided the proximity contacts into 54 distinct time periods representing the day and the night of each day of the study period (27 days). We filtered out ‘passive’ proximity contacts and calculated the cosine similarity index between every possible pair of ‘active’ networks, resulting in a 54x54 matrix of cosine similarity indexes. We performed this test on both weighted and binary networks. As we assume animal space use to be the primary driver of hyrax sociality, we expected binary networks to be very similar when close in time and eventually become less and less similar as they are further apart. Conversely, as hyraxes should re-allocate their social interactions at dawn and dusk to adjust to day-night environmental differences, we expected cosine indexes between weighted networks to be unpredictably high or low over time.

### Comparing ‘active’ network traits between day and night

We calculated node-level and group-level network traits (Table 1) on the 54 time-aggregated networks described above using data-stream permutation-based tests (see *Permutation-based testing*) for paired samples. Nighttime network traits on date n were paired with daytime network traits on dates n and n-1.

### Permutation-based testing

Individuals network traits are correlated due to shared social bonds (Croft *et al.* 2008; Fisher & McAdam 2017). Hence, they violate the primary assumption of data independence, and it is necessary to account for data non-independence when investigating animal sociality. To do so, we used permutations to produce a random distribution of network traits representing a specific null hypothesis and compare it to the network traits measured in the field. Here we assume that hyrax spatial distribution is the main driver of their social interactions.

To test this hypothesis, we used 1,000 focal data-stream permutations (Bejder *et al.* 1998), restricted within groups and within time periods to account for the spatiotemporal structure of the data. If the observed network trait falls within the lower or upper 5% of the random distribution, the null hypothesis simulated by the permutations does not explain the observed data, and the network is influenced by an alternative social process.

Permutation-based tests return a series of dependent uncorrected p-values (one per test) which we combined to assess the overall effect of day/night contrasts on animal social structure using the competitive test with Bonferroni correction for dependent samples from the '*CombinePValue*' R package (Dai *et al.* 2014).

When assessing the statistical significance of cosine similarity indexes on the 54x54 matrice, p-values were not combined, but adjusted using the False Discovery Rate (Benjamini 1995) implemented in the '*stats*' R package (R Core Team 2020). We considered p-value smaller than 0.05 to be significant. All analyses were performed in R version 4.0.1 (R Core Team 2020) .

# Results

## Temporal distribution of hyrax interactions

Raw encounter duration ranged from 11 to 25,605 seconds (~6h), with 95% of all recorded contacts being shorter than 6,576 seconds (1.8h). Hyraxes interacted more during daytime (paired Student test: t=12.734, df=27, p<0.0001, mean difference [95% CI] = 73.18 [61,39; 84.97]). On average, we recorded 62.32 (±19.41) social encounters per night and 135.50 (±31.72) encounters per day. Daytime interactions were shorter on average than nighttime interactions (mean daytime interaction: 393.40 (±659.66) seconds; mean nighttime interaction: 793.93 (±1508.75) seconds; paired Wilcoxon test: V=406, p<0.0001).

## Daytime and nighttime social structure across social contexts

Daytime ‘passive’ networks were correlated with both daytime ($r^2$=0.90, p=0.01) and nighttime ‘active’ networks ($r^2$=0.88, p<0.001). Daytime and nighttime ‘active’ networks predicted each other well ($r^2$=0.95), but this result was only marginally significant according to the permutation test (p=0.08). All other similarity indexes were not significant according to the permutation test (Figure 2).

## Comparing ‘active’ network traits between day and night

At the individual level, hyraxes consistently had fewer ‘active’ connections at night compared to daytime, but the difference in degree centrality was not larger than expected by chance (p=1). Hyraxes displayed lower strength centrality at night compared to daytime ($p<0.001$), meaning they form weaker social bonds at night. Individual eigenvector centrality was higher during nighttime ($p<0.001$), i.e., hyraxes form more connected networks at night. Hyraxes kept interacting with the same individuals between day and night (neighbors' stability: $p<0.001$) (see *Supporting Information*) but allocated their interactions more selectively (individual selectivity: $p<0.001$) (Figure 3).

Social groups were significantly more differentiated at night ($p<0.001$), but edge density did not vary more than expected by chance between daytime and nighttime ($p=0.997$) (Figure 4). All groups displayed lower standard deviation in individual centrality measures (i.e., degree centrality, individual selectivity, eigenvector centrality, see *Supporting information*), meaning groups were more homogeneous at night ($p<0.001$).

### Temporal patterns of 'active' social structure

Almost all pairs of binary networks were more correlated than expected by chance (mean $r^2$ ±sd = 0.57 ±0.16), but binary networks distant in time did not become less correlated than networks close in time. As expected, weighted network similarity indexes were lower than binary network indexes (mean $r^2$ = 0.39 ±0.15). They showed no specific temporal patterns in the way they either correlate or diverge over time (Figure 5).

# Discussion

## Nighttime ‘active’ sociality drives daytime associations

Daytime and nighttime ‘active’ networks are highly correlated, but this level of similarity could result from random associations between individuals of the same group (non-significant permutation test). This suggests that during the day, rock hyraxes preferentially interact with conspecifics with whom they share a sleeping den. Limited access to refuge drives animal movements, and consequently animal sociality, in multiple mammal species (Wolf *et al.* 2007; Podgórski *et al.* 2014; Viblanc *et al.* 2016; Smith *et al.* 2018). At night, den access constrains interactions between members of the same group. In the morning, hyraxes emerge from the den and forage together, rarely further than 15 meters away from a potential shelter (Druce *et al.* 2006). Consequently, while foraging, they favor social behaviours towards individuals who shared their den the night before. We also showed that hyraxes maintain the number and identity of their social partners across day and night, supporting the notion that spatially constrained ‘active’ nighttime associations drive hyrax ‘active’ daytime sociality. Further investigation on how daytime and nighttime social networks influence each other should be carried on in semi-underground species, notably via experimental manipulation of den access.

Surprisingly, daytime ‘passive’ networks accurately predict daytime and nighttime ‘active’ networks, at levels beyond those predicted by hyrax space use (our null hypothesis). Several explanations can be formulated. First, hyraxes that forage together may synchronize their daytime activities as an anti-predator strategy, as seen in other species. For example, guppy shoals living in high-risk conditions display fewer fission events compared to guppies living in low-risk environments (Kelley *et al.* 2011). Roaming away from your social group results in higher exposition to predators whereas sticking together is a good protection against potential threats, despite changes in behavioural activities. Second, as ‘active’ and ‘passive’ daytime social activities are adjacent in time, hyraxes may maintain their social connections because of social continuity. Indeed, they act mostly as a group: they emerge from a shared den in the morning, bask in the sun (reaching hyperthermic levels in the morning, Brown 2003), and then follow a leader to a feeding site (Goll *et al.* 2022) where they forage together. These activities account for most of their ‘active’ daytime sociality. Hyraxes later retreat to cool places where they dissipate the heat accumulated in the morning via passive thermal transfer (Brown 2003). ‘Passive’ proximity contacts mainly occur when they thermoregulate and rest in these cavities, soon after their daily foraging activities. Thus, they maintain the same group when transitioning from morning foraging to afternoon resting. Finally, our study period covers the hyrax annual mating season (Bar Ziv *et al.* 2016). Increased intra-specific competition and aggression during the mating season trigger females to stay together to reduce sexual conflicts in several species. For example, females aggregate together to dilute male sexual attention in red junglefowls (McDonald *et al.* 2019), cockroaches (Stanley *et al.* 2018), and mosquitofish (Pilastro *et al.* 2003). In addition, resident males being very territorial, they drive male competitors away (Schoepf & Schradin 2012) and guard sexually receptive females (Bar Ziv *et al.* 2016), impairing between-group interactions. Consequently, adult hyraxes may maintain their social associations constant throughout the day to cope with heightened levels of sexual competition, predation risk, as a by-product of social continuity, or any combination of these factors, resulting in strong correlations between 'active' and 'passive' interactions during the day.

## Social differentiation is stronger at night

Hyraxes forage outside their den during the day and are therefore exposed to predators. At night, the risk of predation is negligible, but both the risk and the cost of intraspecific aggression increase as limited underground space forces proximity, inducing stress and affecting sleep quality. In free-moving mice, subordinates have shorter deep sleep stages than dominant individuals (Karamihalev *et al.* 2019). In Japanese macaques, familiar individuals sleep better and longer than individuals sleeping with non-native conspecifics (Mochida & Nishikawa 2014). Predation pressure and intra-specific aggression are two factors commonly associated with differentiated social relationships. Thus, some level of social differentiation is expected both at night and during the day. On one hand, under high daytime predation risk, differentiated relationships allow individuals to select social affiliates that are effective in deterring predators. For instance, ungulate species form more modular networks (Sundaresan *et al.* 2007) and Trinidadian guppies become more assortative (Hasenjager & Dugatkin 2017) and more selective (Heathcote *et al.* 2017) in high-risk environments. On the other hand, in contexts where spatial avoidance is not an option and the cost of aggression is high (e.g., dens), differentiated relationships provide support against intra-specific aggression and reduce social stress (Sutcliffe *et al.* 2012; Dunbar

2018). For instance, non-related spider monkeys maintain greater inter-individual distances while sleeping at night than related pairs (Brown 2014), and tufted capuchins sleep closer to matrilineal kin than to unrelated individuals (Di Bitetti *et al.* 2000).

As the fear of being preyed upon usually outweighs the fear of intra-specific aggression, we initially expected the social differentiation to be stronger during the day. Yet, we found that hyraxes are more selective at the individual level and that social relationships are more differentiated at the group level at night. Additionally, the composition of their social environment is almost constant over time, suggesting a stable group composition. Thus, hyraxes reallocate their social interactions towards a few preferred individuals within their group at night. During the day, hyraxes forage together under the surveillance of a sentinel constantly scanning their immediate surroundings (Druce *et al.* 2006; Fanson *et al.* 2011), a behaviour commonly observed in socially cohesive or cooperatively breeding species (Wright *et al.* 2001; Santema & Clutton-Brock 2013). In such groups, information on predators' presence is easier to acquire. Therefore, individuals rely more on group-level cooperation than on a few preferred affiliates, which reduces social differentiation (Moscovice *et al.* 2020). In the rock hyrax, sentinel behaviour combined with a rocky environment rich in hiding spots (Kotler *et al.* 1999) was proven highly effective – adult hyraxes are only rarely preyed upon by terrestrial predators (Margolis 2008). Hence, the effect of predation risk on their social behaviour during the day is lower than expected while no apparent mitigating factors for nighttime social stress are at play. The combination of low predation risk under cooperative anti-predator behaviour during the day and social stress related to social sleeping in a limited space at night therefore drives more differentiated social bonds at night compared to daytime.

Accordingly, populations of hyraxes under higher daytime predation risk should display higher levels of social differentiation during the day than at night, or at least a smaller difference between daytime and nighttime social differentiation compared to our study population. Leopards were the rock hyrax's main terrestrial predator before going extinct in our study area over a decade ago. It is thus likely that our study population used to display different patterns in day/night social differentiation then. It would be interesting to compare daytime and nighttime differences in social structure between populations exposed to varying levels of predation. This could be informative on how short-term network dynamics help wild animals cope with their environment while placing their daytime social structure in its ecological context.

### Does 'active' nighttime sociality present optimal network traits?

At night, hyraxes maintained the structure of their binary network constant (i.e., high stability of neighbours, constant degree centrality and network density) while being less social (i.e., lower strength centrality), more selective of their affiliates (i.e., higher individual selectivity), and yet better connected to the rest of their network (i.e., higher eigenvector centrality). These results suggest that rock hyraxes do not rewire their network between daytime and nighttime but rather redistribute their social interactions within a constant social environment, leading to being better connected to the rest of their group while investing less in socializing. Such nighttime network traits are closer to “optimal” levels reported in studies that, for instance, link high eigenvector centrality to better survival rates (Stanton & Mann 2012; Brent *et al.* 2013a; Brent 2015; Cheney *et al.* 2016) and enhanced information spread (Maharani *et al.* 2015).

Why do hyraxes express “optimal” network traits at night? Maintaining such levels while competing for resources during daytime would be achieved at a high energetic cost since less time is dedicated to sociality (Dunbar 1992; Dunbar *et al.* 2009). Indeed, hyraxes must express a wide range of social behaviours to mitigate predation risk, improve food intake, and increase reproductive success during the day. Furthermore, group-level standard deviations of three individual network traits (i.e., degree centrality, eigenvector centrality and individual selectivity) were significantly lower at night compared to daytime. Indeed, variation in daytime behaviours drives animals to adopt different social niches (Montiglio *et al.* 2013), thus being more socially different from one another compared to nighttime. At night, on the other hand, hyraxes are under negligible predation risk and low thermal stress and do not need to forage, offering more time to socialize. They converge towards network traits closer to “optimal” values, resulting in socially less diverse groups. Considering that egalitarian network positions promote individual survival in rock hyraxes (Barocas *et al.* 2011), this convergence in social behaviours is likely adaptive. Hence, we suggest that nighttime ‘active’ sociality is a favorable time when hyraxes can socialize under negligible external pressures and express “optimal” social behaviours. Group members converge towards similar social behaviours sustaining a well-connected network at a lower social (and potentially energetic) cost than during the day.

Dedicated periods of social interactions exist in multiple animal species, for example, the ‘morning dance’ of Arabian babblers (Zahavi 1990), greeting rituals in mammals living in fission-fusion societies (Aureli & Schaffner 2007; Smith *et al.* 2011) or post-feeding sociality in Barbary macaques (Deag 1985). Observation-based studies revealed that interactions could influence group-level social dynamics across social contexts (Kulahci *et al.* 2018; Canteloup *et al.* 2021; Dragić *et al.* 2021). For instance, allo-grooming networks accurately predict agonistic support in non-human primates (Schino 2007) and subordinate groom dominant individuals to reduce aggression rates both in meerkats (Kutsukake & Clutton-Brock 2006) and Norway rats (Schweinfurth *et al.* 2017). As ‘active’ nighttime sociality in hyraxes is only constrained by space use, relationships built at night likely affect hyrax sociality in other social contexts. Thus, we propose that the nighttime social optimum serves a social function such as described in other species (e.g., social bonds maintenance, aggression reduction, etc.). Investigating context-dependent social structure in this species could thus be of interest and will likely uncover new aspects of hyrax social dynamics. In general, future studies combining the resolution of biologging devices with behaviour classification techniques – such as accelerometers – could shed light on social dynamics in wild species, significantly advancing our understanding of the ecology of group-living animals.

### Persistent topology with unstable edge weights on a monthly scale

The result we reported at the daily scale, i.e., that hyraxes maintain the topology of their network but continuously reallocate their social interactions, was also found at a monthly scale. Thus, hyraxes may actively maintain existing social bonds over time (e.g., monthly scale) while using differentiated relationships to navigate rapidly changing socio-ecological contexts at shorter time scales (e.g., day vs. night ecological conditions). Several recent studies showed that animals maintain a stable social structure across years while displaying variability between seasons (Hamede *et al.* 2009; Henkel *et al.* 2010; Kerth *et al.* 2011; Brent *et al.* 2013b; Borgeaud *et al.* 2017; Nandini *et al.* 2018; Prehn *et al.* 2019). Such patterns improve individual fitness through the establishment of long-lasting and valuable social bonds (Silk *et al.* 2009; Riehl & Strong 2018) while still allowing groups to respond to predictable changes in their physical environment (Barrett *et al.* 2012; Sick *et al.* 2014; Shizuka & Johnson 2020). For example, a seasonal decrease in food resources promotes networks of lower density where group members interact in smaller clusters to decrease intragroup competition for food (Henzi *et al.* 2009). This dual aspect of social relationships bears an adaptive value and must therefore be subjected to selective pressures. Nevertheless, very few studies focused on social dynamics over periods shorter than a season, and to the best of our knowledge, none of them explored the behavioral mechanisms by which seasonal flexibility is achieved but long-term stability is maintained. Our result could be the first step towards understanding this process.

Furthermore, most theories on social stability are based on non-human primates or species known for their complex social structure (Wittemyer *et al.* 2005, 2007; Kerth *et al.* 2011; Gelardi *et al.* 2019; Ripperger & Carter 2021). This bias in studies of animal societies may erroneously suggest that social complexity (see Hobson *et al.* 2019; Kappeler 2019) is a requirement to establish social relationships with this dual nature. Just like complex movement coordination is achieved in bird flocks and fish schools (Bonabeau *et al.* 1997; Ballerini *et al.* 2008), we suggest that 1) long-term population-level social stability can emerge as a by-product of simple daily social tactics, and 2) complex network dynamics can be observed in social species that do not necessarily display complex multilevel social behaviors. More work is needed to understand how complex dynamics emerge at large topological and spatiotemporal scales from short-term patterns. Novel technologies have made data collection simpler for behavioral ecologists, expanding the range of biological questions that can be explored and bringing unprecedented data resolution (Krause *et al.* 2013; Börger *et al.* 2020). Future studies should take advantage of these novel technologies to investigate short-term dynamics of animal societies.

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# Declaration of interest

The authors declare no competing interests.

# References

Aureli, F. & Schaffner, C.M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biol. Lett.*, 3, 147–149.

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., *et al.* (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 1232–1237.

Bar Ziv, E., Ilany, A., Demartsev, V., Barocas, A., Geffen, E. & Koren, L. (2016). Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. *Behav. Ecol. Sociobiol.*, 70, 901–912.

Barocas, A., Ilany, A., Koren, L., Kam, M. & Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS One*, 6, 1–8.

Barrett, L., Peter Henzi, S. & Lusseau, D. (2012). Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. *Philos. Trans. R. Soc. B Biol. Sci.*, 367, 2108–2118.

Barry, R.E. & Mundy, P.J. (2002). Seasonal variation in the degree of heterospecific association of two syntopic hyraxes (Heterohyrax brucei and Procavia capensis) exhibiting synchronous parturition. *Behav. Ecol. Sociobiol.*, 52, 177–181.

Bejder, L., Fletcher, D. & Bräger, S. (1998). A method for testing association patterns of social animals. *Anim. Behav.*, 56, 719–725.

Benjamini, Y. (1995). Controlling the false discovery rate - A practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B*, 57, 289–300.

Di Bitetti, M.S., Vidal, E.M.L., Baldovino, M.C. & Benesovsky, V. (2000). Sleeping site preferences in tufted capuchin monkeys (Cebus apella nigritus). *Am. J. Primatol.*, 50, 257.

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., Aron, S. & Camazine, S. (1997). Self-organization in social insects. *Trends Ecol. Evol.*, 12, 188–193.

Borgeaud, C., Sosa, S., Sueur, C. & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Anim. Behav.*, 134, 155–165.

Börger, L., Bijleveld, A.I., Fayet, A.L., Machovsky-Capuska, G.E., Patrick, S.C., Street, G.M., *et al.* (2020). Biologging Special Feature. *J. Anim. Ecol.*, 89, 6–15.

Boyland, N.K., James, R., Mlynski, D.T., Madden, J.R. & Croft, D.P. (2013). Spatial proximity loggers for recording animal social networks : Consequences of inter-logger variation in performance. *Behav. Ecol. Sociobiol.*, 67, 1877–1890.

Brent, L.J.N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Anim. Behav.*, 103, 211–222.

Brent, L.J.N., Heilbronner, S.R., Horvath, J.E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A.G., *et al.* (2013a). Genetic origins of social networks in rhesus macaques. *Sci. Rep.*, 3, 1042.

Brent, L.J.N., MacLarnon, A., Platt, M.L. & Semple, S. (2013b). Seasonal changes in the structure of rhesus macaque social networks. *Behav. Ecol. Sociobiol.*, 67, 349–359.

Brown, K.J. (2003). Seasonal variation in the thermal biology of the rock hyrax (Procavia capensis), 1–169.

Brown, M.R. (2014). Comparing the Fission-Fusion Dynamics of Spider Monkeys (Ateles geoffroyi) From Day to Night.

Canteloup, C., Cera, M.B., Barrett, B.J. & van de Waal, E. (2021). Processing of novel food reveals payoff and rank-biased social learning in a wild primate. *Sci. Rep.*, 11, 1–13.

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

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

Coe, M.J. (1961). Notes on the habits of the mount kenya hyrax (Procavia johnstoni mackinderi thomas). *Proc. Zool. Soc. London*, 138, 638–644.

Croft, D.P., James, R. & Krause, J. (2008). Introduction to Social Networks. In: *Exploring Animal Social Networks*. Princeton University Press, p. 160.

Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Syst.*, 1695.

Dai, H., Leeder, J.S. & Cui, Y. (2014). A modified generalized fisher method for combining probabilities from dependent tests. *Front. Genet.*, 20, 2–7.

Deag, J.M. (1985). The diurnal patterns of behaviour of the wild Barbary macaque Macaca sylvanus. *J. Zool.*, 206, 403–413.

Dragić, N., Keynan, O. & Ilany, A. (2021). Multilayer social networks reveal the social complexity of a cooperatively breeding bird. *iScience*, 24.

Drewe, J.A., Weber, N., Carter, S.P., Bearhop, S., Harrison, X.A., Dall, S.R.X., *et al.* (2012). Performance of proximity loggers in recording Intra- and Inter-species interactions : A laboratory and field-based validation study. *PLoS One*, 7.

Druce, D.J., Brown, J.S., Castley, J.G., Kerley, G.I.H., Kotler, B.P., Slotow, R., *et al.* (2006). Scale-dependent foraging costs: Habitat use by rock hyraxes (Procavia capensis) determined using giving-up densities. *Oikos*, 115, 513–525.

Dunbar, R.I.M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*, 31, 35–49.

Dunbar, R.I.M. (2018). Social structure as a strategy to mitigate the costs of group living: a comparison of gelada and guereza monkeys. *Anim. Behav.*, 136, 53–64.

Dunbar, R.I.M., Korstjens, A.H. & Lehmann, J. (2009). Time as an ecological constraint. *Biol. Rev.*, 84, 413–429.

Fanson, K. V., Fanson, B.G. & Brown, J.S. (2011). Using path analysis to explore vigilance behavior in the rock hyrax (Procavia capensis). *J. Mammal.*, 92, 78–85.

Fisher, D.N. & McAdam, A.G. (2017). Social traits, social networks and evolutionary biology. *J. Evol. Biol.*, 30, 2088–2103.

Gaston, K.J. (2019). Nighttime ecology: The "nocturnal problem" revisited. *Am. Nat.*, 193, 481–502.

Gelardi, V., Fagot, J., Barrat, A. & Claidière, N. (2019). Detecting social (in)stability in primates from their temporal co-presence network. *Anim. Behav.*, 157, 239–254.

Goll, Y., Bordes, C., Weissman, Y.A., Shnitzer, I., Beukboom, R., Ilany, A., *et al.* (2022). Sex-associated and context-dependent leadership in the rock hyrax. *iScience*, 104063.

Gravett, N., Lyamin, O.I. & Siegel, M. (2012). Sleep in the Rock Hyrax , Procavia capensis, 2012, 155–169.

Hamede, R.K., Bashford, J., McCallum, H. & Jones, M. (2009). Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecol. Lett.*, 12, 1147–1157.

Hasenjager, M.J. & Dugatkin, L.A. (2017). Fear of predation shapes social network structure and the acquisition of foraging information in guppy shoals. *Proc. R. Soc. B Biol. Sci.*, 284.

Heathcote, R.J.P., Darden, S.K., Franks, D.W., Ramnarine, I.W. & Croft, D.P. (2017). Fear of predation drives stable and differentiated social relationships in guppies. *Sci. Rep.*, 7, 1–10.

Henkel, S., Heistermann, M. & Fischer, J. (2010). Infants as costly social tools in male Barbary macaque networks. *Anim. Behav.*, 79, 1199–1204.

Henzi, S.P., Lusseau, D., Weingrill, T., Van Schaik, C.P. & Barrett, L. (2009). Cyclicity in the structure of female baboon social networks. *Behav. Ecol. Sociobiol.*, 63, 1015–1021.

Hobson, E.A., Ferdinand, V., Kolchinsky, A. & Garland, J. (2019). Rethinking animal social complexity measures with the help of complex systems concepts. *Anim. Behav.*, 155, 287–296.

Hoppitt, W. & Farine, D. (2018). Association Indices For Quantifying Social Relationships: How To Deal With Missing Observations Of Individuals Or Groups. *Anim. Behav.*, 136, 227–238.

Ilany, A., Barocas, A., Koren, L., Kam, M. & Geffen, E. (2013). Structural balance in the social networks of a wild mammal. *Anim. Behav.*, 85, 1397–1405.

Kalinka, A.T. & Tomancak, P. (2011). linkcomm: An R package for the generation, visualization, and analysis of link communities in networks of arbitrary size and type. *Bioinformatics*, 27, 2011–2012.

Kappeler, P.M. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol.*, 73.

Karamihalev, S., Flachskamm, C., Eren, N., Kimura, M. & Chen, A. (2019). Social context and dominance status contribute to sleep patterns and quality in groups of freely-moving mice. *Sci. Rep.*, 9, 1–9.

Kelley, J.L., Morrell, L.J., Inskip, C., Krause, J. & Croft, D.P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS One*, 6, e24280.

Kerth, G., Perony, N. & Schweitzer, F. (2011). Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. *Proc. R. Soc. B*, 278, 2761–7.

Koren, L., Mokady, O. & Geffen, E. (2008). Social status and cortisol levels in singing rock hyraxes. *Horm. Behav.*, 54, 212–216.

Kotler, B.P., Brown, J.S. & Knight, M.H. (1999). Habitat and patch use by hyraxes: There's no place like home? *Ecol. Lett.*, 2, 82–88.

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S. & Rutz, C. (2013). Reality mining of animal social systems. *Trends Ecol. Evol.*, 28, 541–551.

Kulahci, I.G., Ghazanfar, A.A. & Rubenstein, D.I. (2018). Knowledgeable Lemurs Become More Central in Social Networks. *Curr. Biol.*, 28, 1306-1310.e2.

Kummer, H. & Kurt, F. (1963). Social units of free-living population of hamadryas baboons. *Folia Primotology*, 4–19.

Kutsukake, N. & Clutton-Brock, T.H. (2006). Social functions of allogrooming in cooperatively breeding meerkats. *Anim. Behav.*, 72, 1059–1068.

Lesku, J.A., Aulsebrook, A.E., Kelly, M.L. & Tisdale, R.K. (2019). *Evolution of Sleep and Adaptive Sleeplessness*. *Handb. Behav. Neurosci.* 1st edn. Elsevier B.V.

Lima, S.L., Rattenborg, N.C., Lesku, J.A. & Amlaner, C.J. (2005). Sleeping under the risk of predation. *Anim. Behav.*, 70, 723–736.

Maharani, W., Adiwijaya & Gozali, A.A. (2015). Degree centrality and eigenvector centrality in twitter. *Proc. 2014 8th Int. Conf. Telecommun. Syst.*

*Serv. Appl. TSSA 2014*, 10–14.

Margolis, E. (2008). Dietary composition of the wolf Canis lupus in the Ein Gedi area according to analysis of their droppings (in Hebrew). In: *Proceedings of 45th Meeting of the Israel Zoological Society*.

Matsuda, I., Tuuga, A. & Higashi, S. (2010). Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: Why do they sleep alone inland on flooded days? *Ecol. Res.*, 25, 475–482.

McDonald, G.C., Spurgin, L.G., Fairfield, E.A., Richardson, D.S. & Pizzari, T. (2019). Differential female sociality is linked with the fine-scale structure of sexual interactions in replicate groups of red junglefowl, Gallus gallus. *Proc. R. Soc. B Biol. Sci.*, 286.

Mochida, K. & Nishikawa, M. (2014). Sleep duration is affected by social relationships among sleeping partners in wild Japanese macaques. *Behav. Processes*, 103, 102–104.

Montiglio, P.-O., Ferrari, C. & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philos. Trans. R. Soc. B Biol. Sci.*, 368, 20120343.

Moscovice, L.R., Sueur, C. & Aureli, F. (2020). How socio-ecological factors influence the differentiation of social relationships: An integrated conceptual framework. *Biol. Lett.*, 16.

Mulavwa, M.N., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Mwanza, N.N. & Furuichi, T. (2010). Nest groups of wild bonobos at Wamba: Selection of vegetation and tree species and relationships between nest group size and party size. *Am. J. Primatol.*, 72, 575–586.

Nandini, S., Keerthipriya, P. & Vidya, T.N.C. (2018). Group size differences may mask underlying similarities in social structure: A comparison of female elephant societies. *Behav. Ecol.*, 29, 145–159.

Ogawa, H., Idani, G., Moore, J., Pintea, L. & Hernandez-Aguilar, A. (2007). Sleeping Parties and nest distribution of chimpanzees in the Savanna woodland, Ugalla, Tanzania. *Int. J. Primatol.*, 28, 1397–1412.

Ogawa, H. & Takahashi, H. (2002). Triadic positions of Tibetan macaques huddling at a sleeping site. *Int. J. Primatol.*, 24, 591–606.

Park, O., Barden, A. & Williams, E. (1940). Studies in Nocturnal Ecology, IX. Further Analysis of Activity of Panama Rain Forest Animals. *Ecology*, 21, 122.

Pilastro, A., Benetton, S. & Bisazza, A. (2003). Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish Gambusia holbrooki. *Anim. Behav.*, 65, 1161–1167.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L. & Jędrzejewska, B. (2014). Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. *PLoS One*, 9, 1–11.

Prehn, S.G., Laesser, B.E., Clausen, C.G., Jønck, K., Dabelsteen, T. & Brask, J.B. (2019). Seasonal variation and stability across years in a social network of wild giraffe. *Anim. Behav.*, 157, 95–104.

R Core Team, R. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Riehl, C. & Strong, M.J. (2018). Stable social relationships between unrelated females increase individual fitness in a cooperative bird. *Proc. R. Soc. B Biol. Sci.*, 285.

Ripperger, S.P. & Carter, G.G. (2021). Social foraging in vampire bats is predicted by long-term cooperative relationships. *PLoS Biol.*, 19, 1–17.

Santema, P. & Clutton-Brock, T. (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Anim. Behav.*, 85, 655–661.

Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behav. Ecol.*, 18, 115–120.

Schoepf, I. & Schradin, C. (2012). Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (Rhabdomys pumilio). *J. Anim. Ecol.*, 81, 649–656.

Schreier, A.L. & Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *Am. J. Phys. Anthropol.*, 148, 580–588.

Schweinfurth, M.K., Stieger, B. & Taborsky, M. (2017). Experimental evidence for reciprocity in allogrooming among wild-type Norway rats. *Sci. Rep.*, 7, 1–8.

Shizuka, D. & Johnson, A.E. (2020). How demographic processes shape animal social networks. *Behav. Ecol.*, 31, 1–11.

Sick, C., Carter, A.J., Marshall, H.H., Knapp, L.A., Dabelsteen, T. & Cowlishaw, G. (2014). Evidence for varying social strategies across the day in chacma baboons. *Biol. Lett.*, 10, 3–6.

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

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., *et al.* (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B Biol. Sci.*, 276, 3099–3104.

Silk, M.J., Weber, N., Steward, L.C., Delahay, R.J., Croft, D.P., Hodgson, D.J., *et al.* (2017). Seasonal variation in daily patterns of social contacts in the European badger meles meles. *Ecol. Evol.*, 7, 9006–9015.

Smith, J.E., Gamboa, D.A., Spencer, J.M., Travenick, S.J., Ortiz, C.A., Hunter, R.D., *et al.* (2018). Split between two worlds: Automated sensing reveals links between above- and belowground social networks in a free-living mammal. *Philos. Trans. R. Soc. B Biol. Sci.*, 373.

Smith, J.E., Powning, K.S., Dawes, S.E., Estrada, J.R., Hopper, A.L., Piotrowski, S.L., *et al.* (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Anim. Behav.*, 81, 401–415.

Snyder-Mackler, N., Beehner, J.C. & Bergman, T.J. (2012). Defining Higher Levels in the Multilevel Societies of Geladas (Theropithecus gelada). *Int. J. Primatol.*, 33, 1054–1068.

Stanley, C.R., Liddiard Williams, H. & Preziosi, R.F. (2018). Female clustering in cockroach aggregations—A case of social niche construction? *Ethology*, 124, 706–718.

Stanton, M.A. & Mann, J. (2012). Early Social Networks Predict Survival in Wild Bottlenose Dolphins. *PLoS One*, 7, 1–6.

Sundaresan, S.R., Fischhoff, I.R., Dushoff, J. & Rubenstein, D.I. (2007). Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia*, 151, 140–149.

Sutcliffe, A., Dunbar, R., Binder, J. & Arrow, H. (2012). Relationships and the social brain: Integrating psychological and evolutionary perspectives. *Br. J. Psychol.*, 103, 149–168.

Takahashi, H. (1997). Huddling relationships in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. *Primates*, 38, 57–68.

Tougeron, K. & Abram, P.K. (2017). An Ecological Perspective on Sleep Disruption. *Am. Nat.*, 190, 55–66.

Viblanc, V.A., Pasquaretta, C., Sueur, C., Boonstra, R. & Dobson, F.S. (2016). Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness. *Behav. Ecol.*, 27, arw098.

Wild, F. (2020). lsa: Latent Semantic Analysis. R package version 0.73.2. https://CRAN.R-project.org/package=lsa.

Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.*, 69, 1357–1371.

Wittemyer, G., Getz, W.M., Vollrath, F. & Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: A contribution to conservation behavior. *Behav. Ecol. Sociobiol.*, 61, 1919–1931.

Wolf, J.B.W., Mawdsley, D., Trillmich, F. & James, R. (2007). Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim. Behav.*, 74, 1293–1302.

Wright, J., Berg, E., De Kort, S.R., Khazin, V. & Maklakov, A.A. (2001). Cooperative sentinel behaviour in the Arabian babbler. *Anim. Behav.*, 62, 973–979.

Zahavi, A. (1990). Arabian babbler. In: *Cooperative Breeding in Birds* (eds. Staceyp, B. & Koenigw, D.). Cambridge University Press, London, pp. 103-130.

# Tables

Table 1: Network trait definitions and topological level of interest

| Trait | Definition | Level |
|---|---|---|
| Degree centrality | Number of connections of a node | Node |
| Strength centrality | Sum of a node’s connection weights | |
| Eigenvector centrality | Measure of how well a node is connected to the rest of the network considering its connections and the connections of its neighbours. | |
| Neighbors’ stability | Proportion of social partners an individual keeps interacting with between two consecutive time periods. | |
| Individual selectivity | Coefficient of variation of a node’s edge weights | |
| Network density | Proportion of existing edges within a group of nodes | Group |
| Social differentiation | Coefficient of variation of the weights of all edges within a group | |
| Group homogeneity | Standard deviation of degree centrality, eigenvector centrality and individual selectivity within a group | |

# Figures:

Figure 1: Proximity-based social network from 28 Sirtrack proximity loggers aggregated over the full study period (27 days). Circles depict individual rock hyraxes. Colours indicate individual assignment to communities based on a community-detection algorithm. Pie charts represent the proportion of social interactions a hyrax maintains with each community.

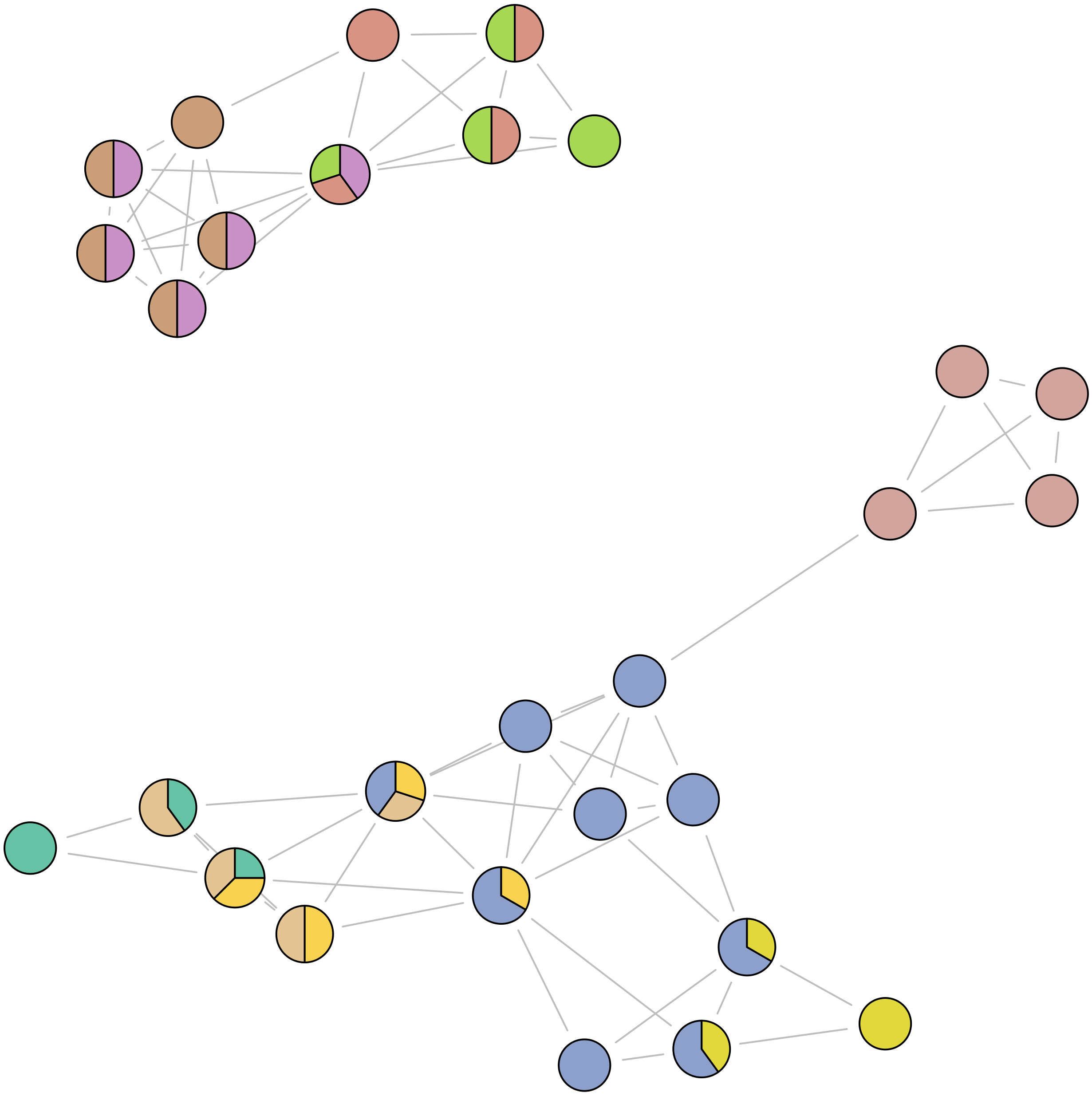

Figure 2: Correlation matrix between social networks built on different times of the day (night or day) and across social contexts (interactions longer or shorter than 25 minutes). ‘*’: The permutation test is significant at the level of 0.05.

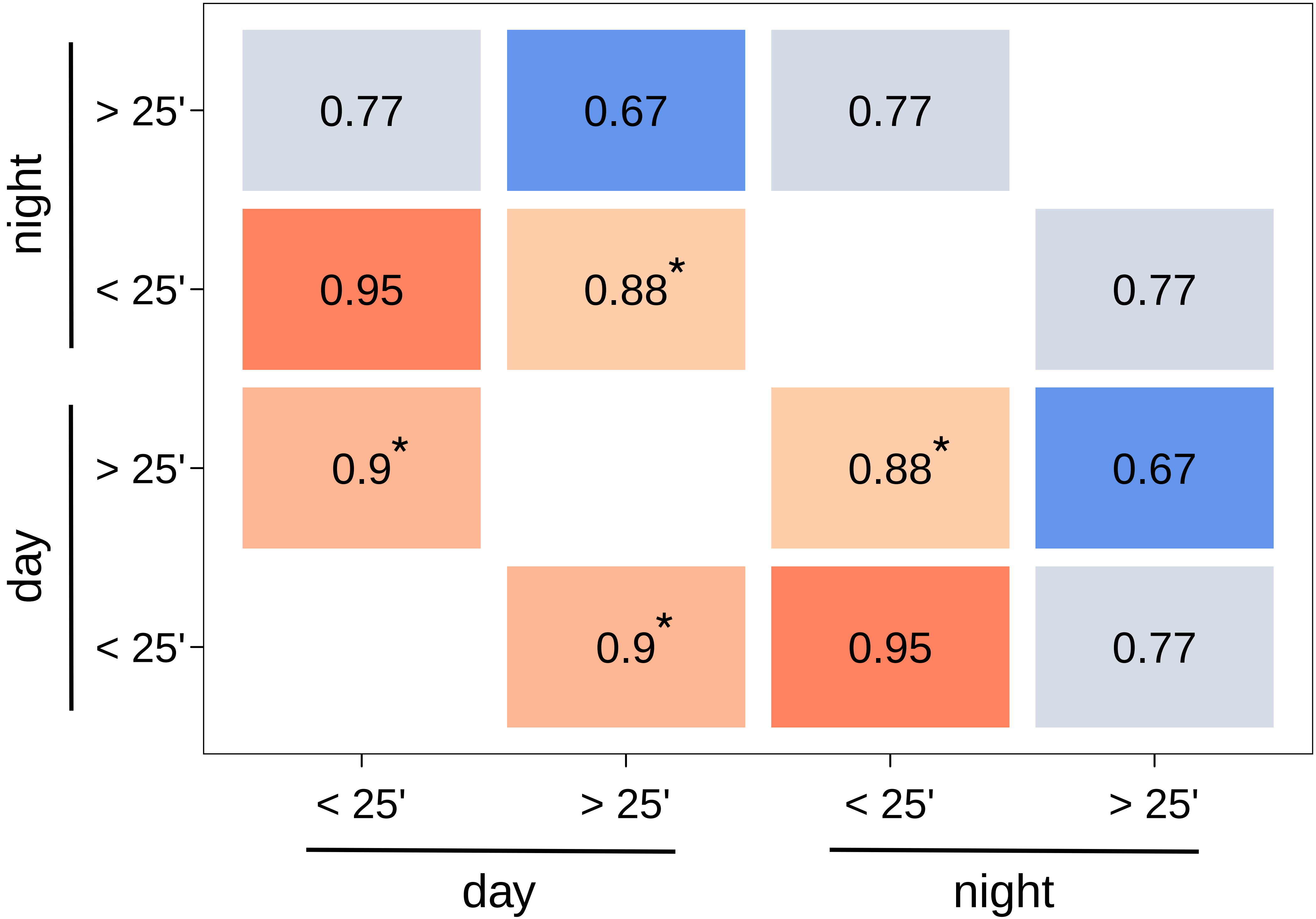
night
> 25'
< 25'
day
> 25'
< 25'
0.77
0.67
0.77
0.95
0.88*
0.77
0.9*
0.88*
0.67
0.9*
0.95
0.77
< 25'
> 25'
< 25'
> 25'
day
night

Figure 3: Mean individual network traits over time (left) and associated cumulated distributions (right) during the day (orange) and at night (blue). Significance level of day-night differences according to permutation-based tests: ‘ns’: non-significant; ‘***’: $p<0.001$.

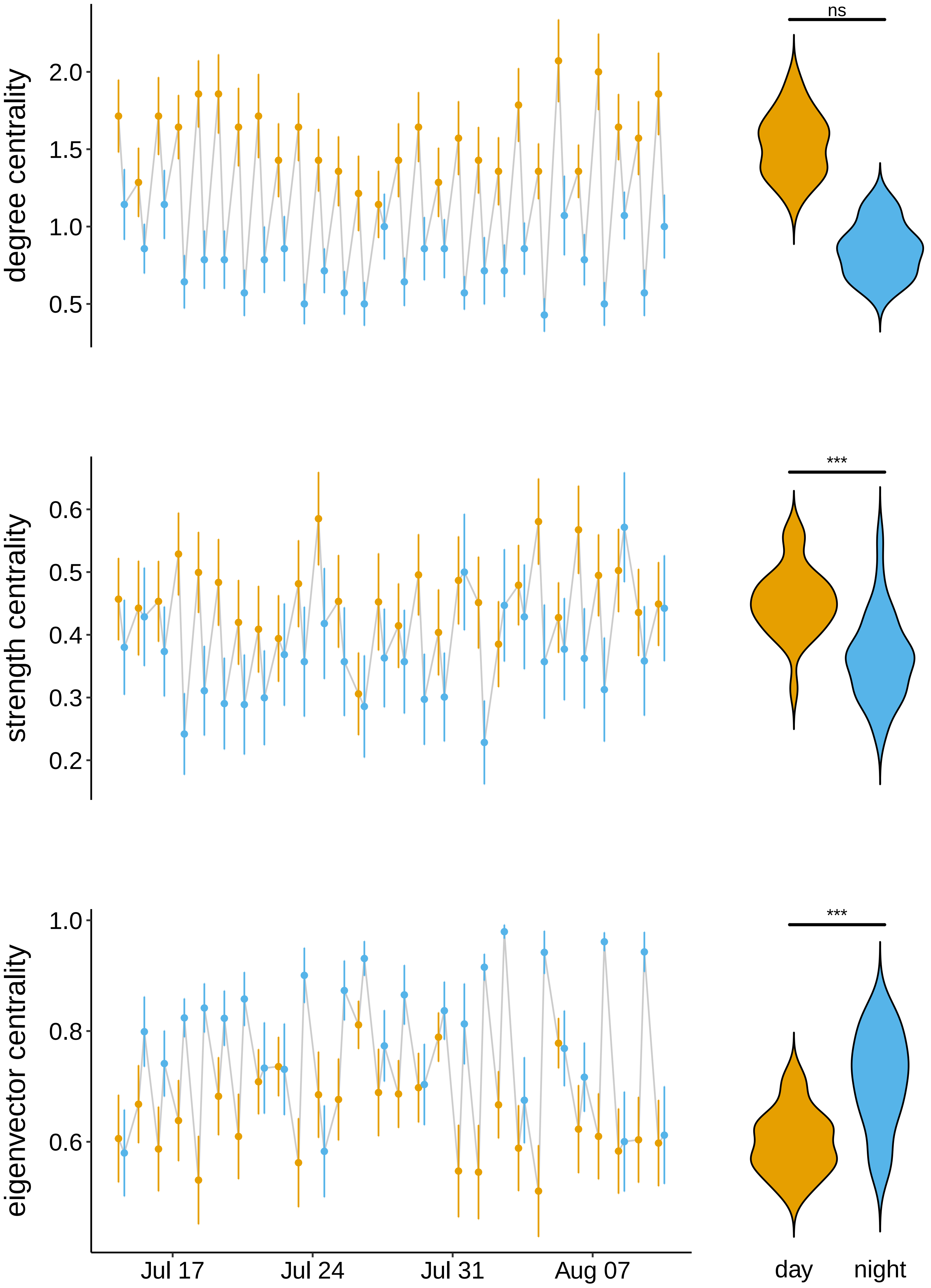
degree centrality
2.0
1.5
1.0
0.5
ns
strength centrality
0.6
0.5
0.4
0.3
0.2
***
eigenvector centrality
1.0
0.8
0.6
***
Jul 17
Jul 24
Jul 31
Aug 07
day
night

Figure 4: Mean group-level network traits and individual selectivity over time (left) and associated cumulative distributions (right) during the day (orange) and at night (blue). Significance level of day-night differences according to permutation-based tests: ‘ns’, non-significant; ‘***’, $p<0.001$.

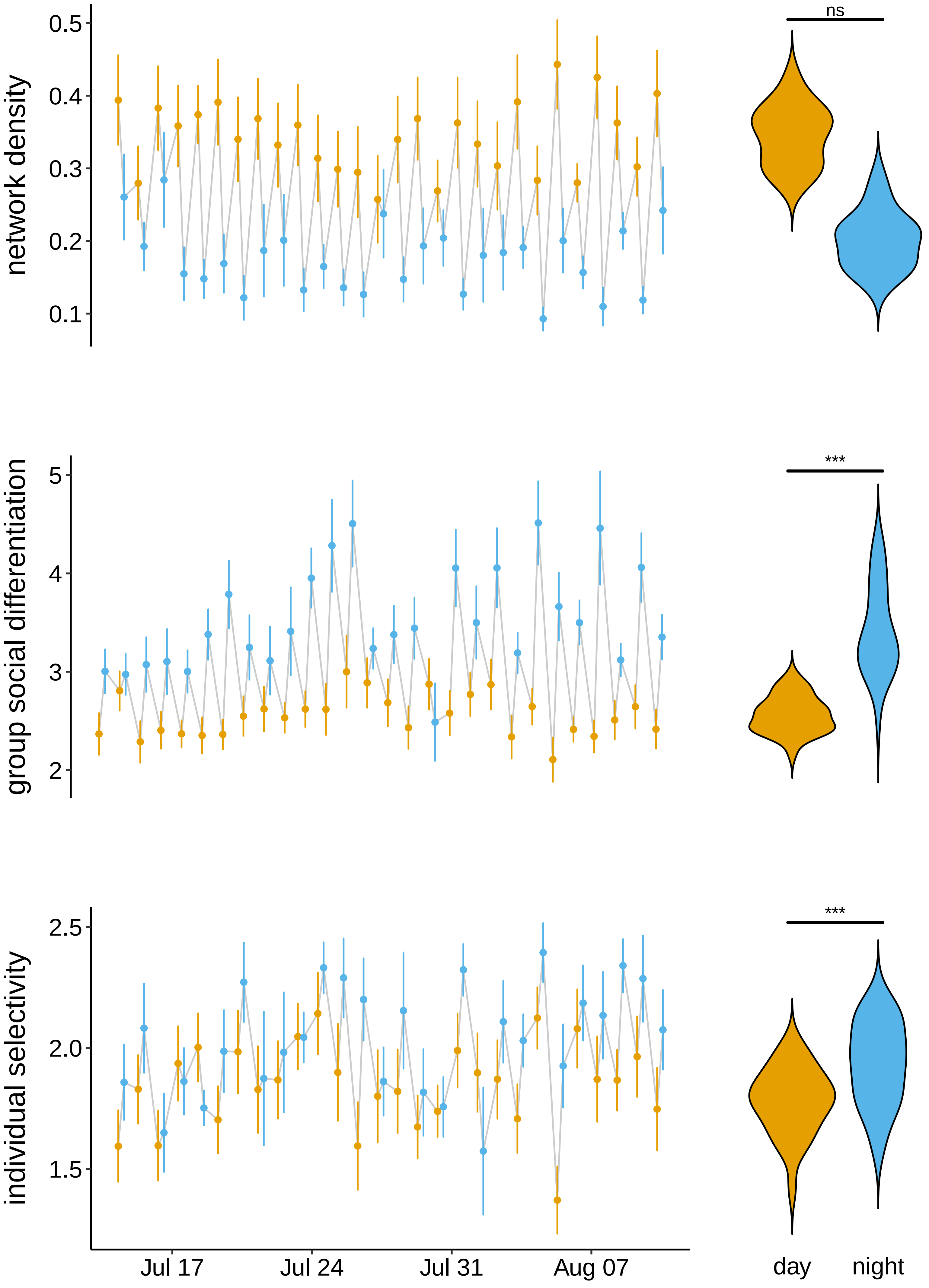
network density
0.5
0.4
0.3
0.2
0.1
ns
group social differentiation
5
4
3
2
***
individual selectivity
2.5
2.0
1.5
***
Jul 17
Jul 24
Jul 31
Aug 07
day
night

Figure 5: Pairwise cosine similarity indexes between all possible pairs of social networks (left) and associated permutation-based p-values (right) for weighted networks (top) and binary networks (bottom).


Cosine similarity indexes
Associated p−values
Weighted networks
Binary networks
Aug 07
Jul 31
Jul 24
Jul 17
Jul 17
Jul 24
Jul 31
Aug 07
Similarity index
0
0.48
0.91
Observed value is:
Lower than random
Higher than random
Non significant