

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

3 Camille N. M. Bordes<sup>1</sup>, bordescamille93@gmail.com

4 Rosanne Beukeboom<sup>1</sup>, rosanne.beukeboom@gmail.com

5 Yael Goll<sup>2</sup>, yael.goll@gmail.com

6 Lee Koren<sup>1</sup>, Lee.Koren@biu.ac.il

7 Amiyaal Ilany<sup>1</sup>, amiyaal@gmail.com

8

9 <sup>1</sup> Faculty of Life Sciences, Bar-Ilan University (Israel)

10 <sup>2</sup> School of Zoology, Tel Aviv University (Israel)

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13 CB, RB, and YG collected the data. CB and AI designed the study. CB

14 designed and performed the analysis. CB wrote the manuscript. AI and LK

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16 manuscript.

17

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19 [https://github.com/camillebordes/Hyrax\\_daily\\_SND](https://github.com/camillebordes/Hyrax_daily_SND)

20

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28 **Corresponding author:**

29 Amiyaal Ilany

30 Faculty of Life Sciences, Bar-Ilan University (Israel)

31 972-3-5318218 (office); 972-3-5317926 (lab)

32 amiyaal@gmail.com

33

34

## 35 Abstract

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

## 50 Introduction

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

60           Sleeping in groups also exposes individuals to intra-specific aggression,  
61 but it is a lesser risk than being predated while asleep. Hence, most diurnal  
62 social species maintain sociality at night to limit predation risk (Lima *et al.*  
63 2005) despite the cost of social stress. Several species of apes form larger  
64 social groups at night than during the day (Ogawa *et al.* 2007; Mulavwa *et al.*  
65 2010) and become more tolerant of conspecifics' proximity when sleeping in  
66 dangerous habitats (Kummer & Kurt 1963; Matsuda *et al.* 2010; Schreier &  
67 Swedell 2012). When the risk of predation is higher than the risk of intra-  
68 specific aggression at night, sleeping groups become larger, denser, and less  
69 selective (Ogawa & Takahashi 2002). Conversely, when the risk of predation  
70 becomes negligible compared to the risk of being attacked by a conspecific,  
71 daytime groups either split into sub-units, sometimes leading individuals to  
72 sleep alone (Snyder-Mackler *et al.* 2012), or adapt their sleeping phases. For  
73 example, unfamiliar macaques synchronize their wakefulness more than  
74 individuals coming from the same natal group (Mochida & Nishikawa 2014),

75 which reduces the risk of intraspecific aggression from unfamiliar  
76 individuals.

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

89         Despite the importance of nighttime ecology (Park *et al.* 1940; Gaston  
90 2019), little attention has been given to animal sociality outside their main  
91 activity periods. For decades, data related to animal sociality have been  
92 collected via direct behavioural observations, which are spatially and  
93 temporally constrained by observers' abilities. Consequently, studies on the  
94 sociality of wild animals have mostly been limited to diurnal species (easier  
95 to observe) when observations were possible (mainly daytime and in open  
96 spaces). The recent revolution of automated data collection has increased the  
97 accuracy, resolution, and spatiotemporal range of behavioural data,  
98 facilitating the tracking of social interactions around the clock (Krause *et al.*  
99 2013; Börger *et al.* 2020). Yet, few biologging-based studies investigated the

100 structure of animal social networks outside their main activity period (but see  
101 Silk *et al.* 2017 and Smith *et al.* 2018). This gap is important to address  
102 considering the importance of sleep for individual fitness (Tougeron &  
103 Abram 2017).

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

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

124 underground. Consequently, they are a good candidate species to explore  
125 nighttime sociality and how it relates to daytime social structure.

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

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

## 147 Materials and methods

### 148 Data collection and sampling

149 We conducted fieldwork in the Ein Gedi Nature Reserve in Israel (31°  
150 28' N, 35° 24' E) on two distinct study sites located approximately 2.5 km  
151 apart. Between March and August 2017, we studied 83 wild rock hyraxes, 37  
152 of which were old enough to receive a biogger. Hyraxes were trapped  
153 between March and June according to previously published protocols (Koren  
154 *et al.* 2008). Briefly we set 30 live box traps in strategic trapping sites before  
155 sunrise for about 4 hours. Any trapped hyrax heavier than 1.8 kg was  
156 anaesthetized using 0.1mg/kg of ketamine hydrochloride (intramuscular  
157 injection) and fitted with Sirtrack E2C-171-A proximity bioggers. Having  
158 assessed loggers' quality under laboratory conditions (Boylard *et al.* 2013)  
159 before deployment, we deployed loggers that consistently performed well  
160 together, whereas pairs of loggers showing poor performance were deployed  
161 in different study sites to minimize their chances of encounter.

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

169 Social network analysis

170 Constructing proximity-based networks

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

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

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

191       Calculating network traits

192       Community structure is a crucial feature of social network analysis. We  
193 used the Overlapping Cluster Detection algorithm from the ‘*linkcomm*’ R  
194 package (Kalinka & Tomancak 2011) to detect nested overlapping  
195 communities in the study population (Figure 1). As some individuals interact  
196 with multiple groups every day, they can be affiliated to several communities  
197 at the same time. We defined their group as the union of all their communities.  
198 Preliminary exploration of proximity data revealed that 7 proximity events  
199 (0.04%) occurred between the assigned groups. We calculated 5 node-level  
200 and 2 group-level network traits (Table 1) using the ‘*igraph*’ R package  
201 (Csardi & Nepusz 2006). We also calculated the standard deviation of 3  
202 individual network traits within groups (i.e., degree centrality, eigenvector  
203 centrality, and individual selectivity).

204       Data analysis

205       Discriminating between ‘passive’ and ‘active’ sociality at night

206       Sleep is associated with lower levels of awareness (Siegel 2008), which  
207 affects individuals’ likelihood to initiate interactions or end existing ones.  
208 When two awake individuals are engaged in a long interaction, they may  
209 break the ongoing encounter at any moment. But once animals are asleep, the  
210 contact lasts as long as both individuals remain unconscious. Consequently,  
211 social encounters recorded when two individuals are asleep are not the result  
212 of a repeated and active choice to remain near each other (‘active’ contacts).  
213 Rather, they are the result of a social behaviour expressed while awake and  
214 being carried out after losing consciousness (‘passive’ contacts). Due to their

215 length, ‘passive’ contacts strongly affect the social structure of an aggregated  
216 network, which may mask the ‘active’ sociality expressed in-between  
217 sleeping bouts. Since nighttime social structure is predominantly sleep-  
218 related in rock hyraxes, comparing social behaviours between daytime and  
219 nighttime requires ignoring sleeping associations. We analyzed the  
220 correlation between networks based on interactions of different lengths to  
221 identify ‘passive’ associations. Our results showed that a threshold of 25  
222 minutes in interaction length accurately discriminates between two different  
223 social structures, prompting us to divide contacts into ‘passive’ (>25 minutes)  
224 and ‘active’ (<25 minutes) in the rest of this study (*Supporting information*).

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

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

238 Comparing ‘active’ social networks across days

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

251 Comparing ‘active’ network traits between day and night

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

257 Permutation-based testing

258 Individuals network traits are correlated due to shared social bonds (Croft  
259 *et al.* 2008; Fisher & McAdam 2017). Hence, they violate the primary  
260 assumption of data independence, and it is necessary to account for data non-

261 independence when investigating animal sociality. To do so, we used  
262 permutations to produce a random distribution of network traits representing  
263 a specific null hypothesis and compare it to the network traits measured in the  
264 field. Here we assume that hyrax spatial distribution is the main driver of their  
265 social interactions.

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

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

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

282

## 283 Results

### 284 Temporal distribution of hyrax interactions

285         Raw encounter duration ranged from 11 to 25,605 seconds (~6h), with  
286 95% of all recorded contacts being shorter than 6,576 seconds (1.8h). Hyraxes  
287 interacted more during daytime (paired Student test:  $t=12.734$ ,  $df=27$ ,  
288  $p<0.0001$ , mean difference [95% CI] = 73.18 [61,39; 84.97]). On average, we  
289 recorded 62.32 ( $\pm 19.41$ ) social encounters per night and 135.50 ( $\pm 31.72$ )  
290 encounters per day. Daytime interactions were shorter on average than  
291 nighttime interactions (mean daytime interaction: 393.40 ( $\pm 659.66$ ) seconds;  
292 mean nighttime interaction: 793.93 ( $\pm 1508.75$ ) seconds; paired Wilcoxon  
293 test:  $V=406$ ,  $p<0.0001$ ).

### 294 Daytime and nighttime social structure across social contexts

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

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

302         At the individual level, hyraxes consistently had fewer ‘active’  
303 connections at night compared to daytime, but the difference in degree  
304 centrality was not larger than expected by chance ( $p=1$ ). Hyraxes displayed

305 lower strength centrality at night compared to daytime ( $p < 0.001$ ), meaning  
306 they form weaker social bonds at night. Individual eigenvector centrality was  
307 higher during nighttime ( $p < 0.001$ ), i.e., hyraxes form more connected  
308 networks at night. Hyraxes kept interacting with the same individuals  
309 between day and night (neighbors' stability:  $p < 0.001$ ) (see *Supporting*  
310 *Information*) but allocated their interactions more selectively (individual  
311 selectivity:  $p < 0.001$ ) (Figure 3).

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

318 Temporal patterns of 'active' social structure

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

## 325 Discussion

326 Nighttime ‘active’ sociality drives daytime associations

327 Daytime and nighttime ‘active’ networks are highly correlated, but this  
328 level of similarity could result from random associations between individuals  
329 of the same group (non-significant permutation test). This suggests that  
330 during the day, rock hyraxes preferentially interact with conspecifics with  
331 whom they share a sleeping den. Limited access to refuge drives animal  
332 movements, and consequently animal sociality, in multiple mammal species  
333 (Wolf *et al.* 2007; Podgórski *et al.* 2014; Viblanc *et al.* 2016; Smith *et al.*  
334 2018). At night, den access constrains interactions between members of the  
335 same group. In the morning, hyraxes emerge from the den and forage  
336 together, rarely further than 15 meters away from a potential shelter (Druce  
337 *et al.* 2006). Consequently, while foraging, they favor social behaviours  
338 towards individuals who shared their den the night before. We also showed  
339 that hyraxes maintain the number and identity of their social partners across  
340 day and night, supporting the notion that spatially constrained ‘active’  
341 nighttime associations drive hyrax ‘active’ daytime sociality. Further  
342 investigation on how daytime and nighttime social networks influence each  
343 other should be carried on in semi-underground species, notably via  
344 experimental manipulation of den access.

345 Surprisingly, daytime ‘passive’ networks accurately predict daytime  
346 and nighttime ‘active’ networks, at levels beyond those predicted by hyrax  
347 space use (our null hypothesis). Several explanations can be formulated. First,  
348 hyraxes that forage together may synchronize their daytime activities as an

349 anti-predator strategy, as seen in other species. For example, guppy shoals  
350 living in high-risk conditions display fewer fission events compared to  
351 guppies living in low-risk environments (Kelley *et al.* 2011). Roaming away  
352 from your social group results in higher exposition to predators whereas  
353 sticking together is a good protection against potential threats, despite  
354 changes in behavioural activities. Second, as ‘active’ and ‘passive’ daytime  
355 social activities are adjacent in time, hyraxes may maintain their social  
356 connections because of social continuity. Indeed, they act mostly as a group:  
357 they emerge from a shared den in the morning, bask in the sun (reaching  
358 hyperthermic levels in the morning, Brown 2003), and then follow a leader to  
359 a feeding site (Goll *et al.* 2022) where they forage together. These activities  
360 account for most of their ‘active’ daytime sociality. Hyraxes later retreat to  
361 cool places where they dissipate the heat accumulated in the morning via  
362 passive thermal transfer (Brown 2003). ‘Passive’ proximity contacts mainly  
363 occur when they thermoregulate and rest in these cavities, soon after their  
364 daily foraging activities. Thus, they maintain the same group when  
365 transitioning from morning foraging to afternoon resting. Finally, our study  
366 period covers the hyrax annual mating season (Bar Ziv *et al.* 2016). Increased  
367 intra-specific competition and aggression during the mating season trigger  
368 females to stay together to reduce sexual conflicts in several species. For  
369 example, females aggregate together to dilute male sexual attention in red  
370 junglefowls (McDonald *et al.* 2019), cockroaches (Stanley *et al.* 2018), and  
371 mosquitofish (Pilastro *et al.* 2003). In addition, resident males being very  
372 territorial, they drive male competitors away (Schoepf & Schradin 2012) and  
373 guard sexually receptive females (Bar Ziv *et al.* 2016), impairing between-

374 group interactions. Consequently, adult hyraxes may maintain their social  
375 associations constant throughout the day to cope with heightened levels of  
376 sexual competition, predation risk, as a by-product of social continuity, or any  
377 combination of these factors, resulting in strong correlations between ‘active’  
378 and ‘passive’ interactions during the day.

379 Social differentiation is stronger at night

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

399 2018). For instance, non-related spider monkeys maintain greater inter-  
400 individual distances while sleeping at night than related pairs (Brown 2014),  
401 and tufted capuchins sleep closer to matrilineal kin than to unrelated  
402 individuals (Di Bitetti *et al.* 2000).

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

424 predator behaviour during the day and social stress related to social sleeping  
425 in a limited space at night therefore drives more differentiated social bonds at  
426 night compared to daytime.

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

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

440       At night, hyraxes maintained the structure of their binary network  
441 constant (i.e., high stability of neighbours, constant degree centrality and  
442 network density) while being less social (i.e., lower strength centrality), more  
443 selective of their affiliates (i.e., higher individual selectivity), and yet better  
444 connected to the rest of their network (i.e., higher eigenvector centrality).  
445 These results suggest that rock hyraxes do not rewire their network between  
446 daytime and nighttime but rather redistribute their social interactions within  
447 a constant social environment, leading to being better connected to the rest of  
448 their group while investing less in socializing. Such nighttime network traits

449 are closer to “optimal” levels reported in studies that, for instance, link high  
450 eigenvector centrality to better survival rates (Stanton & Mann 2012; Brent  
451 *et al.* 2013a; Brent 2015; Cheney *et al.* 2016) and enhanced information  
452 spread (Maharani *et al.* 2015).

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

473 well-connected network at a lower social (and potentially energetic) cost than  
474 during the day.

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

496 Persistent topology with unstable edge weights on a monthly scale

497 The result we reported at the daily scale, i.e., that hyraxes maintain the  
498 topology of their network but continuously reallocate their social interactions,  
499 was also found at a monthly scale. Thus, hyraxes may actively maintain  
500 existing social bonds over time (e.g., monthly scale) while using  
501 differentiated relationships to navigate rapidly changing socio-ecological  
502 contexts at shorter time scales (e.g., day vs. night ecological conditions).  
503 Several recent studies showed that animals maintain a stable social structure  
504 across years while displaying variability between seasons (Hamede *et al.*  
505 2009; Henkel *et al.* 2010; Kerth *et al.* 2011; Brent *et al.* 2013b; Borgeaud *et*  
506 *al.* 2017; Nandini *et al.* 2018; Prehn *et al.* 2019). Such patterns improve  
507 individual fitness through the establishment of long-lasting and valuable  
508 social bonds (Silk *et al.* 2009; Riehl & Strong 2018) while still allowing  
509 groups to respond to predictable changes in their physical environment  
510 (Barrett *et al.* 2012; Sick *et al.* 2014; Shizuka & Johnson 2020). For example,  
511 a seasonal decrease in food resources promotes networks of lower density  
512 where group members interact in smaller clusters to decrease intragroup  
513 competition for food (Henzi *et al.* 2009). This dual aspect of social  
514 relationships bears an adaptive value and must therefore be subjected to  
515 selective pressures. Nevertheless, very few studies focused on social  
516 dynamics over periods shorter than a season, and to the best of our knowledge,  
517 none of them explored the behavioral mechanisms by which seasonal  
518 flexibility is achieved but long-term stability is maintained. Our result could  
519 be the first step towards understanding this process.

520           Furthermore, most theories on social stability are based on non-human  
521 primates or species known for their complex social structure (Wittemyer *et*  
522 *al.* 2005, 2007; Kerth *et al.* 2011; Gelardi *et al.* 2019; Ripperger & Carter  
523 2021). This bias in studies of animal societies may erroneously suggest that  
524 social complexity (see Hobson *et al.* 2019; Kappeler 2019) is a requirement  
525 to establish social relationships with this dual nature. Just like complex  
526 movement coordination is achieved in bird flocks and fish schools (Bonabeau  
527 *et al.* 1997; Ballerini *et al.* 2008), we suggest that 1) long-term population-  
528 level social stability can emerge as a by-product of simple daily social tactics,  
529 and 2) complex network dynamics can be observed in social species that do  
530 not necessarily display complex multilevel social behaviors. More work is  
531 needed to understand how complex dynamics emerge at large topological and  
532 spatiotemporal scales from short-term patterns. Novel technologies have  
533 made data collection simpler for behavioral ecologists, expanding the range  
534 of biological questions that can be explored and bringing unprecedented data  
535 resolution (Krause *et al.* 2013; Börger *et al.* 2020). Future studies should take  
536 advantage of these novel technologies to investigate short-term dynamics of  
537 animal societies.

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544 Declaration of interest

545 The authors declare no competing interests.

546

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## 831 Tables

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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	

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