

## Research



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# Using network synchrony to identify drivers of social dynamics

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Social animals frequently show dynamic social network patterns, the consequences of which are felt at the individual and group level. It is often difficult, however, to identify what drivers are responsible for changes in these networks. We suggest that patterns of network synchronization across multiple social groups can be used to better understand the relative contributions of extrinsic and intrinsic drivers. When groups are socially separated, but share similar physical environments, the extent to which network measures across multiple groups covary (i.e. network synchrony) can provide an estimate of the relative roles of extrinsic and intrinsic drivers. As a case example, we use allogrooming data from three adjacent vervet monkey groups to generate dynamic social networks. We found that network strength was strongly synchronized across the three groups, pointing to shared extrinsic environmental conditions as the driver. We also found low to moderate levels of synchrony in network modularity, suggesting that intrinsic social processes may be more important in driving changes in subgroup formation in this population. We conclude that patterns of network synchronization can help guide future research in identifying the proximate mechanisms behind observed social dynamics in animal groups.

## 1. Introduction

Group-living animals experience repeated interactions with others and can develop relationships that wax and wane through time [1,2]. This sets up a social environment that is intrinsically dynamic. The patterning of social interactions has been shown to correlate with components of fitness [3–6], by mediating, in part, the risks of predation [7] and infectious disease [8], as well as thermoregulatory efficiency [9]. Social network analysis has been used to describe the social structures that emerge from social behaviours and to locate individuals in the structure of the larger social group [10–12]. While earlier work generally focused on static networks, the need to better understand how individuals achieve and regulate their network position [13–16] has led to an increase in the attention paid to dynamic social networks where it's possible to track temporal shifts [17–19].

Much of the work on dynamic social networks has focused solely on intrinsic group processes such as the influence of current social structure on subsequent social behaviour [20,21]. Similarly, recent work on multilayer networks has documented how changes in one network layer may drive changes in another [22–25]. There is also, however, good evidence to suggest that factors extrinsic to the group, such as changes in the physical environment [1,26–29], may also underpin social network dynamics.

Given this, it is surprising that there has been little examination of the relative influence of—or interaction between—intrinsic and extrinsic factors in the dynamics of social network structure (though see [1,30,31]). This is relevant because, without an understanding of whether and how extrinsic and intrinsic factors operate within a given context, our analyses are vulnerable to misinterpretation. That is, we may mistake extrinsically driven shifts in network structure, over which animals have little control, for intrinsic shifts that reflect individual strategies or tactics for improving network position. This in turn may lead us to mischaracterize the mechanisms by which social network position gives rise to any fitness-related benefits.

One way to assess the relative roles of intrinsic and extrinsic drivers is to measure patterns of synchronization across multiple groups that share a physical environment, as has been done in systems biology and population ecology [32,33]. Where multiple social groups share the same local environment, extrinsic environmental factors, such as rainfall, temperature and general food availability, would—*sensu lato*—be held in common by them all. If extrinsic factors, therefore, are largely responsible for changes to social dynamics within groups, we would expect changes to network structures to be synchronized across them. That is, the changes seen in one group would be mirrored by equivalent changes in another, which we refer to as network synchrony. Here, network synchrony refers to network measures that show simultaneous temporal covariation across different groups. By contrast, if network changes are driven by factors intrinsic to each group, such as the specificities of the individuals and the combined characteristics of its members, we would anticipate lower levels of synchrony across groups on the expectation that intrinsic dynamics would tend to decouple groups from one other, while also possibly giving rise to idiosyncratic responses to environmental change. Such decoupling is likely to be increased where individual social behaviours not only create the social structures but are, in turn, influenced by them (i.e. where there are social feedback loops: [22,34,35]). Measuring network synchrony across groups thus makes possible an understanding of the relative roles of intrinsic and extrinsic drivers without any prior need to specify the specific mechanisms that might be involved. Once the magnitude of synchrony is known, it becomes, in principle, easier to then identify and tease apart the influence of specific contributors, and reveal how sensitive social organization is to environmental perturbation.

Here, we use 3.5 years of social data on three adjacent groups of vervet monkeys (*Chlorocebus pygerythrus*), whose territories overlap substantially, to estimate the extent of cross-group synchrony in the social network structure of female grooming interactions. To do so, we consider variation within and between groups with respect to two network measures. (i) We first quantify the synchrony in mean grooming strength across groups (i.e. the mean of the weighted degree of each node in the network). Mean grooming strength relies on direct network connections and we use this as our measure of the extent to which individual grooming behaviours increase or decrease within groups. (ii) We then quantify the synchrony in grooming modularity across groups. Modularity relies on indirect network connections and measures the extent to which the allocation of grooming generates subgroups within social networks, and how delineations of subgroups increase or decrease. After generating time-series data for the two network measures for each group, we then estimate network synchrony using multi-variate time-series models to determine inter-group correlations. Mean grooming strength allows us to test how intrinsic/extrinsic factors drive grooming effort; that is, how much time individuals are spending in close proximity physically grooming others. Grooming modularity allows us to assess how intrinsic/extrinsic factors drive the allocation of that grooming effort; that is who is grooming whom, how frequently and how this allocation results in distinct subgrouping within the larger group. Given there are many possible network measures, we have chosen to focus on grooming strength and modularity as both are associated in the literature with infectious disease

transmission. Grooming strength, in particular, provides an estimate of how much time individuals are spending close to others, while grooming modularity provides an estimate of group structure that has been associated with transmission [8,36]. By estimating the relative roles of intrinsic and extrinsic drivers on these particular network measures, we aim to develop a better understanding of how social behaviour can impact infectious disease transmission within social groups in changing environments.

## 2. Methods

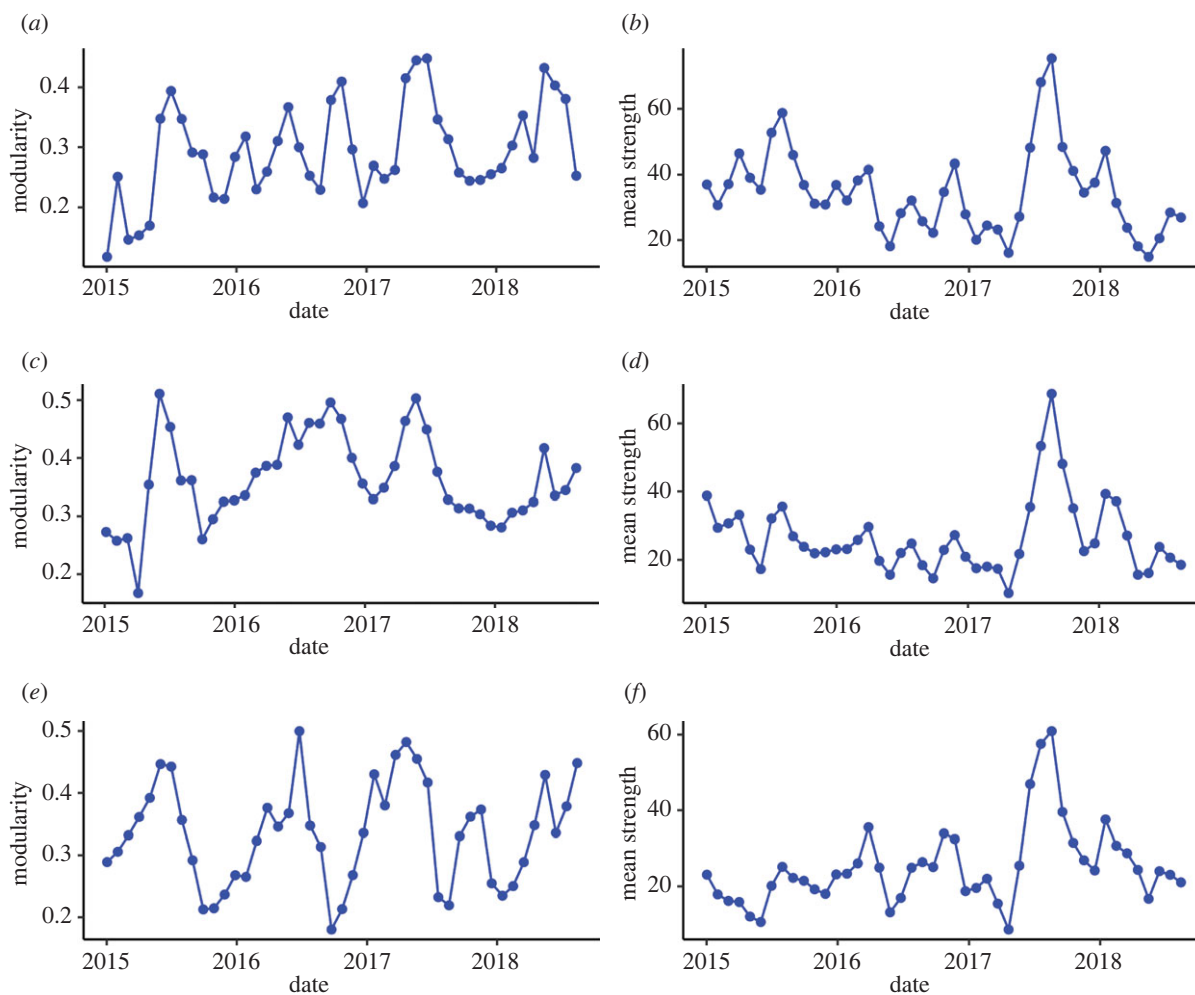
### (a) Study population and network construction

Grooming data were collected using scan samples [37] of all visible individuals during a 10 min block initiated every 30 min during each 10 h field day from three groups of vervet monkeys (see, for example, [38]) as part of a long-term field project in the semi-arid Karoo ecosystem of South Africa [39]. The three groups are referred to herein as PT, RBM and RST; the abbreviations have no relevance beyond being a unique identifier. All field assistants were trained to visually recognize all adult individuals. We used data collected from January 2015 to November 2018, comprising 21 404 observed grooming events between females. The number of females in each group was PT mean = 12 (95% CI: 8, 17), RBM mean = 15 (95% CI: 7, 22) and RST mean = 17 (95% CI: 8, 22), and the sex ratio was PT mean = 0.56 (95% CI: 0.45, 0.73), RBM mean = 0.56 (95% CI: 0.46, 0.73) and RST mean = 0.54 (95% CI: 0.42, 0.58).

We used the package ‘nefTS’ [40] in R v. 3.5.2 [41] to construct grooming networks and extract network measures as time series for each group. We aggregated networks into 60-day windows, as correlations between the observed and bootstrapped networks indicated that shorter time scales resulted in noisy estimates of strength and modularity (electronic supplementary material, figure S1). Each aggregate window was then shifted by 30-days, resulting in a time series of 45 networks covering 1260 days (figure 1). To estimate mean network strength, we used the ‘strength’ function, and for network modularity, we used the ‘walktrap’ algorithm, in the ‘igraph’ package in R [42]. As grooming is a directed behaviour, we calculate strength of a node using both in- and out- edges (i.e. the sum of the two). Similarly, the walktrap algorithm uses the sum of in- and out- edges between two nodes when detecting community membership to calculate network modularity. To aid in interpretation, networks showing high/low mean grooming strength and high/low grooming modularity are provided in the electronic supplementary material, figure S2.

### (b) Study design

By using a study design that looks at network synchronization across multiple social groups that share similar physical environments, we aim to estimate the extent to which network changes can be attributed to extrinsic drivers. However, there are other variables that might inflate network synchronization. Under conditions where individuals from one network can be assumed not to interact with individuals in another network, the observed dynamics of each network can be considered separately. This greatly facilitates the distinction between potential extrinsic and intrinsic drivers of network dynamics. In field settings where the assumption of complete separation is not always possible, it is important to recognize that interactions between groups could increase the observed synchronization between networks. That is, there are shared events that may affect more than one group simultaneously as a consequence of non-environmental factors (e.g. territorial disputes between groups). In our study



**Figure 1.** Time series of network measures for three vervet monkey groups: (a,b) PT, (c,d) RBM and (e,f) RST. The date marks the start of a 60-day window that was used to construct a grooming network. For each network, (a,c,e) grooming modularity and (b,d,f) mean grooming strength were calculated. (Online version in colour.)

system, we focused on female grooming networks, which are directed to others only within the same group, which mitigates the potential inflation in synchrony of any interactions across groups. Females do, however, interact across groups during aggressive inter-group encounters. These aggressive interactions between groups, and the subsequent within-group grooming that occurs afterwards, are a potential driver of network synchrony between two groups. Similarly, as males often disperse from one neighbouring group to another [43], it is possible that periods of high male dispersal might drive synchrony in female grooming patterns across groups as each deals with an influx of new male members. Finally, as vervets are seasonal breeders, network synchronization across groups could also be a result of grooming patterns due to shared influx of new female members as infants from a given yearly cohort mature into the adult network. Consequently, we use a multi-variate approach to account for these potential drivers of between-group patterns with the aim of estimating the remaining network synchrony that is due to extrinsic drivers.

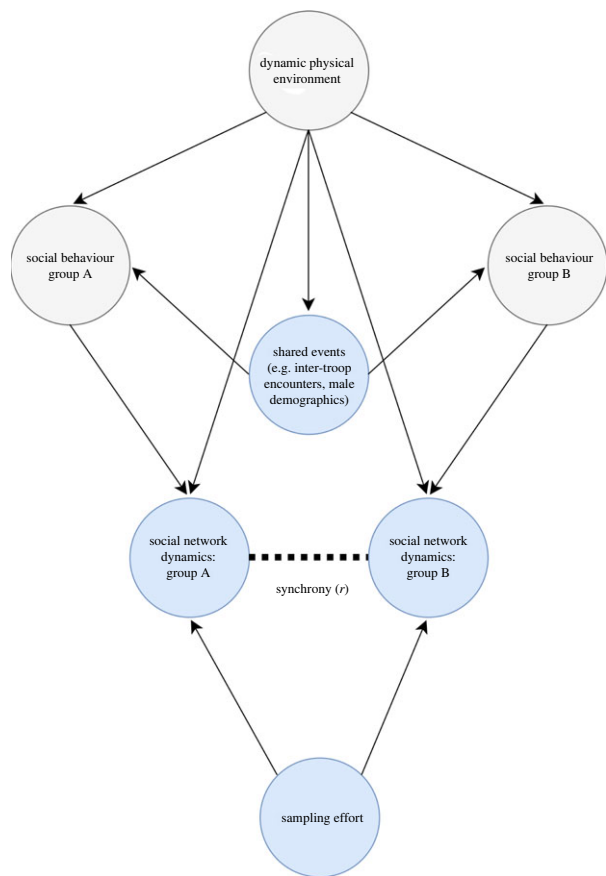
As an initial step in measuring synchrony between social network measures of groups, we constructed a directed acyclic graph to outline our assumed causal structure of how network synchrony is generated between any two groups [44,45]. Our measured variables are the social network measures from each group, shared events we'd like to account for (e.g. inter-troop encounters (ITEs)), as well as information about the sampling effort used to generate these data. Following from the introduction, we assume that, beyond sampling effort and shared events, network measures are influenced by intrinsic social behaviour within a group, as well as extrinsic environmental factors (figure 2). In the case of extrinsic environmental factors,

we assume that they influence network measures both directly and indirectly through intrinsic social behaviour (figure 2). This assumed causal structure represents our hypothesis for how network synchronization emerges. Following from this hypothesized causal structure, our predictions are that the increased influence of extrinsic environmental drivers as well as shared events will increase network synchronization between groups, while the increased influence of intrinsic social behaviour within a group will decrease network synchronization.

Following Young *et al.*'s [46] findings that the probability of performing social behaviours, such as grooming, was influenced by food availability in this population, we predict (i) that mean grooming strength will show synchrony across groups, because this is at least partially driven by this extrinsic factor. By contrast, we expect (ii) that grooming modularity will show no synchrony across groups, as it is likely to be less sensitive to extrinsic environmental conditions and more sensitive to intrinsic social history and characteristics of a group. This is because, as a measure that is reliant on the distribution and strengths of all dyadic relationships in the group, grooming modularity is highly dependent on the particulars of who is currently grooming whom. Therefore, if past dyadic interactions influence future dyadic interactions, we expect changes in grooming modularity to be dependent principally on the specific history of dyadic relationships within a social group.

### (c) Statistical methods

Given that sampling effort can influence network measures, any increase or decrease in sampling effort shared by groups could artificially inflate synchrony across groups (figure 2). Shared



**Figure 2.** Causal diagram of network synchrony between two social groups. The blue circles represent measured variables, and the grey circles represent unmeasured variables. The arrows indicate the assumed direction of influence, and the dashed line indicates the estimate of synchrony. (Online version in colour.)

events between groups (such as ITEs) or events experienced by all groups (male migration, group size changes due to seasonal breeding) could similarly result in increased synchronization between groups. To measure the synchrony due to extrinsic drivers alone, we therefore constructed a model that accounts for sampling effort, number of ITEs, number of males within the group and group size. By accounting for these variables, we are able to estimate the covariance of the remaining unexplained variance. This covariance estimation is our target measure of synchronization between the groups. To accomplish this, we specified a multi-variate Student's  $t$  distribution where the scaled and centred network measures from each social group were used as the response variables. To model the mean of each response, we estimated an intercept and the effect of sampling effort, ITEs, male migrations and group size on network measures. Using this multi-variate student- $t$  distribution, we could then estimate the covariance between the errors, as follows:

$$\begin{pmatrix} V_{1,t} \\ V_{2,t} \\ V_{3,t} \end{pmatrix} = \text{MVStudentT} \left( \begin{pmatrix} \mu_{1,t} \\ \mu_{2,t} \\ \mu_{3,t} \end{pmatrix}, \Sigma \right) \quad \text{Likelihood}$$

$$\begin{aligned} \mu_{1,t} &= a_1 + b_1 * \text{effort}_{1,t} + b_2 * \text{ITE} + b_3 * \text{males} + b_4 * \text{size} + \text{gp}(\text{date}) \\ \mu_{2,t} &= a_2 + b_2 * \text{effort}_{2,t} + b_2 * \text{ITE} + b_3 * \text{males} + b_4 * \text{size} + \text{gp}(\text{date}) \\ \mu_{3,t} &= a_3 + b_3 * \text{effort}_{3,t} + b_2 * \text{ITE} + b_3 * \text{males} + b_4 * \text{size} + \text{gp}(\text{date}) \end{aligned} \quad \text{Mean}$$

$$\Sigma = \begin{bmatrix} \sigma_{1,1} & \sigma_{1,2} & \sigma_{1,3} \\ \sigma_{2,1} & \sigma_{2,2} & \sigma_{2,3} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_{3,3} \end{bmatrix} \quad \text{Covariance}$$

where  $V_{1,t}$  is the network measure of group 1 at time  $t$ ,  $\mu_{1,t}$  is the estimated mean of group 1 at time  $t$  and  $\Sigma$  is the covariance matrix. Each estimated mean ( $\mu_{1,t}$ ) is a function of the overall

group mean ( $a_1$ ), the sampling effort and a Gaussian process that accounts for the autocorrelation in network measures through time ( $\text{gp}(\text{date})$ ). The covariance term  $\sigma_{1,2}$  is the covariance between network measures in group 1 and 2, and is equal to the covariance  $\sigma_{2,1}$  (i.e. covariance between groups 2 and 1). We then used these covariance estimates to calculate correlations ( $r$ ) between the group network measures, and these correlations were used as our measure of synchrony between groups. To run the model, we used 'brms' [47] and provide the code in electronic supplementary material, S2.

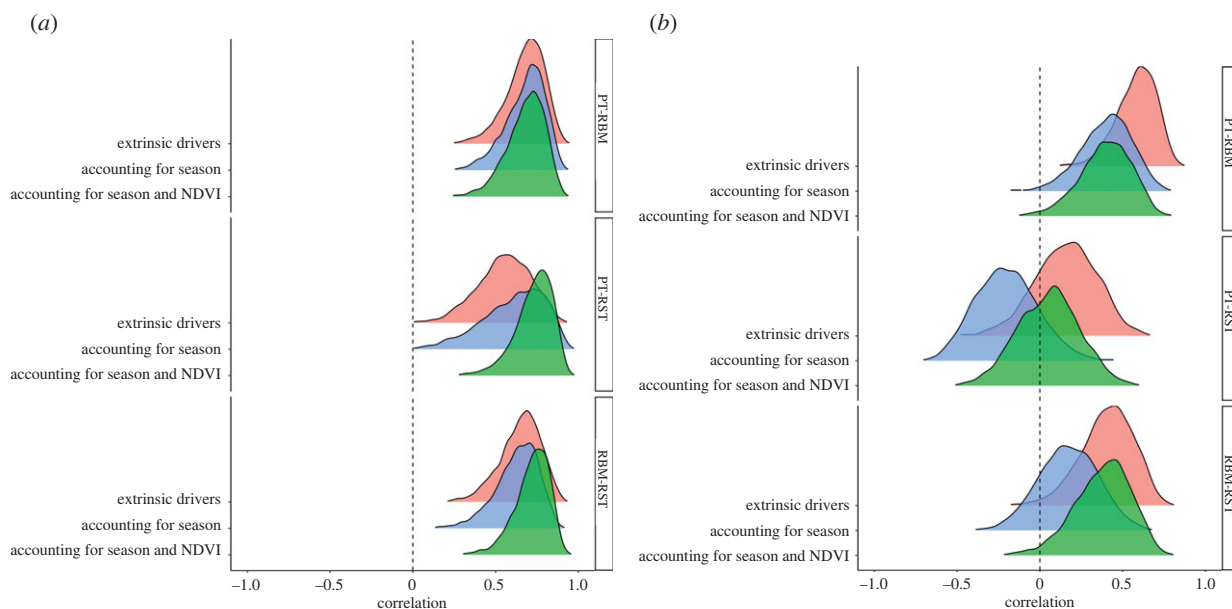
Having measured the magnitude of synchrony using the models above, we then performed a second set of analyses in which we added extrinsic variables that potentially could generate synchrony in social network dynamics. If the addition of these variables explains some portion of the variation in network measures across groups, it will alter the estimated synchrony between social networks by changing the remaining error and the covariance between the errors. Specifically, if we find a reduction in synchrony when an extrinsic variable is added, it suggests that this variable is responsible for similar changes in each social network and will account for the correlation found in the errors (e.g. if the mean grooming strength of both group A and B consistently goes up in response to the added variable). If, on the other hand, we find that the addition of the extrinsic variable increases the estimated synchrony between the networks, it suggests that the variable is responsible for dissimilar changes in each social network and will account for unsynchronized patterns in the errors (e.g. the mean grooming strength of group A consistently responds to this variable by going up, while group B does not respond to this variable). This approach therefore allows us, where network synchrony is detected, to identify its potential drivers.

To monitor shifts in synchrony, we added variables one at a time, starting with day of year, followed by the normalized difference vegetation index (NDVI). This allowed us to first estimate synchrony due to the effect of season, followed by the effect of NDVI, an estimate of food availability that is also influenced by season (see [46] for more details). For season, we specified a cyclic cubic regression spline to allow for nonlinear effects. To visualize the model outcomes, we use marginal mean plots to show how each group is predicted to respond to changes in each environmental variable.

To ensure the proposed modelling approach can accurately estimate network synchrony, we simulated grooming data where we could control the source and amount of synchronization between two groups. Using these simulated data, we ran our proposed method to assess whether, with our sample size and modelling approach, we could accurately estimate synchrony while accounting for different causes of synchrony (e.g. accounting for variation in sampling effort, and due to food availability). We confirm that we could do so and present these simulated tests of our proposed model in the electronic supplementary material, S3).

### 3. Results

We found that groups exhibited high synchrony in mean grooming strength, with an estimated correlation between the groups of  $r_{\text{PTRBM}} = 0.68$ ,  $r_{\text{PTRST}} = 0.55$  and  $r_{\text{RBM,RST}} = 0.65$  (figure 3a and table 1). This implied that extrinsic factors are important drivers of changes to mean grooming strength. When testing for specific extrinsic drivers, we found that after accounting for season and food availability (NDVI), estimates of correlation did not decrease, but rather increased or remained the same:  $r_{\text{PT,RBM}} = 0.68$ ,  $r_{\text{PT,RST}} = 0.73$  and  $r_{\text{RBM,RST}} = 0.72$  (figure 3a and table 1). To identify the



**Figure 3.** Posterior density estimates of synchrony between grooming networks of the three groups (PT, RBM and RST): (a) mean grooming strength and (b) grooming modularity. Estimates of synchrony due to extrinsic drivers are made for each of the three group combinations (red density plot), followed by estimates of synchrony after accounting for any synchronization between the groups due to seasonal drivers (blue density plot), and both seasonal and NDVI drivers (green density plot). (Online version in colour.)

causes of the observed increase/decrease in synchrony, we examined the estimated group response to the environmental variables tested. We found that NDVI had differing impacts on mean grooming strength depending on the group, with groups either increasing or decreasing grooming in response to increasing NDVI (figure 4a). This explains the increased correlation in the errors when NDVI was accounted for in these models, whereas we found little variation in a seasonal response for mean grooming strength (figure 4b).

For grooming modularity, we found that groups exhibited low to moderate estimates of synchrony:  $r_{PT,RBM} = 0.58$ ,  $r_{PT,RST} = 0.16$  and  $r_{RBM,RST} = 0.41$  (figure 3b and table 1). This indicated a more variable influence of extrinsic factors on network modularity. When testing for specific extrinsic drivers, we found a consistent drop in correlation when season and NDVI were included:  $r_{PT,RBM} = 0.40$ ,  $r_{PT,RST} = 0.05$  and  $r_{RBM,RST} = 0.38$  (figure 3 and table 1). To identify the causes of the observed decrease in synchrony, we examined the estimated group response to the environmental variables tested. We found that NDVI had differing impacts on grooming modularity, where increased NDVI was associated with decreased modularity in two groups but had relatively little impact on the third (figure 4c). This explains the increased correlation in the errors when NDVI was accounted for in these models. Conversely, we found very similar seasonal responses across all three groups for network modularity (figure 4d), which explains the decreased correlation in the errors when season was accounted for in the grooming modularity model.

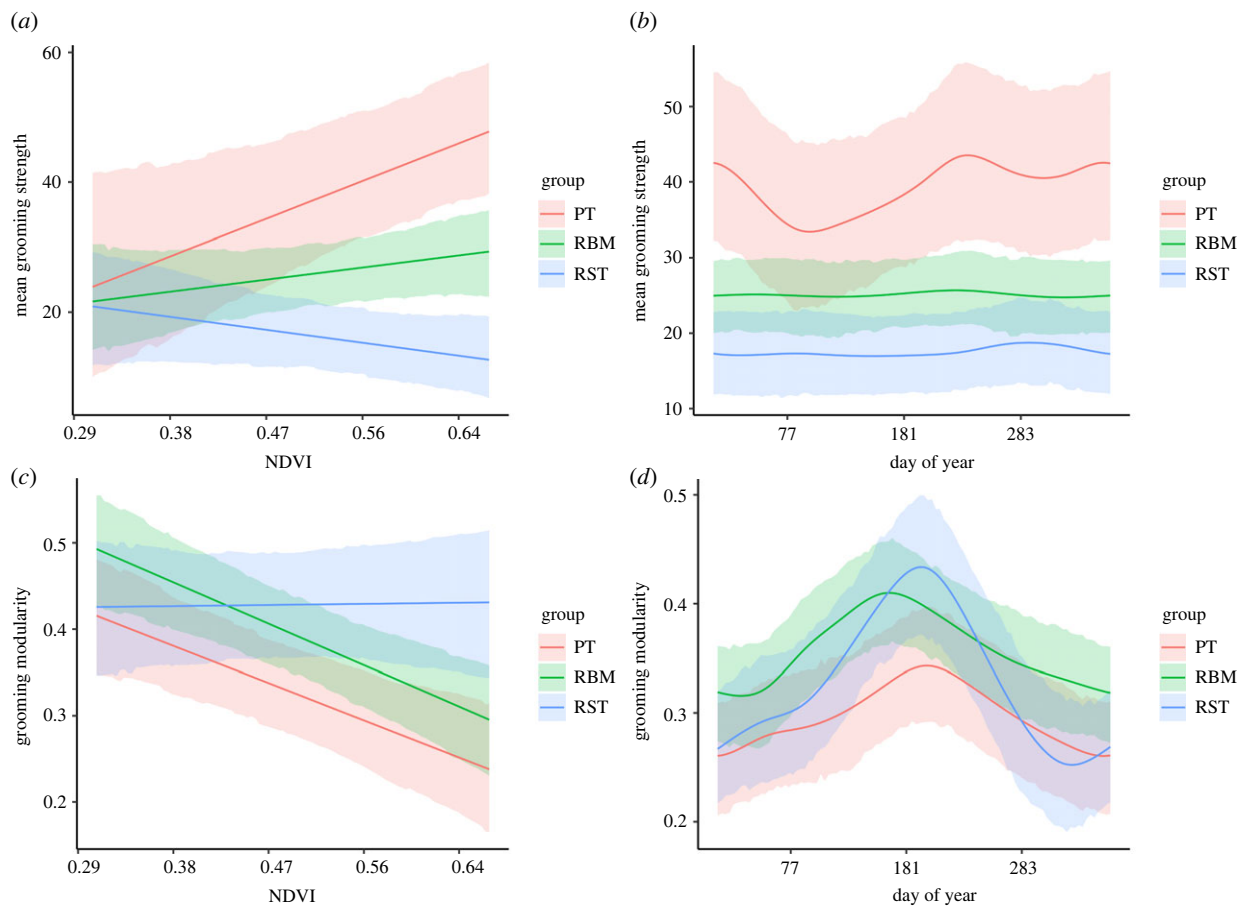
## 4. Discussion

In quantifying the social network dynamics of three vervet groups that share similar physical environments, we identified high synchrony in mean grooming strength, and lower synchrony in how that grooming behaviour generated distinct subgroups within the groups (i.e. grooming

modularity). This supports the argument that extrinsic and intrinsic factors play different roles in driving observed changes in these social network measures.

The high level of synchrony in mean grooming strength ( $r_{avg} = 0.63$ ) within these groups suggests that observed changes were driven primarily by extrinsic drivers (figure 3a). In attempting to identify the particular extrinsic drivers that were responsible, we found that accounting for season and NDVI did not explain the estimated synchronization, which stayed the same or increased ( $r_{avg} = 0.71$ ), suggesting that these factors were therefore unlikely to be the primary cause of grooming synchrony across these three groups. Interestingly, the increase in synchrony of mean grooming strength, once NDVI was accounted for, was a consequence of groups responding to NDVI, although not in the same way (figure 3a). This indicates that differences in intrinsic variables within each group (e.g. specific characteristics of individuals and specific social histories) are likely to underpin the response to NDVI. Our results also showed a relatively limited role of season on mean grooming strength (figure 3b), indicating that physical environmental variables, such as temperature or daylight, are unlikely to be driving this observed synchronization between the groups. Our results therefore do not identify a potential driver for this level of synchronization across the groups. One explanation might be that extreme weather events such as short heavy rainfalls, windstorms or short periods of extreme heat/cold might be driving changes in mean grooming strength across all three groups. The distribution of these extreme weather events might not show a strong seasonal pattern and could explain why accounting for season using day-of-year did not reduce the estimated synchronization. This explanation, however, is only speculation and would need to be tested more formally in future work.

By contrast (figure 3b), we found relatively lower estimates of synchronization across groups for grooming modularity ( $r_{avg} = 0.38$ ). That is, while the dynamics of mean grooming strength were highly synchronized across



**Figure 4.** Estimated influence of environmental variables on network measures: (a) NDVI on mean grooming strength, (b) day of the year on mean grooming strength, (c) NDVI on grooming modularity and (d) day of year on grooming modularity. (Online version in colour.)

**Table 1.** Model estimates of synchrony ( $r$ ) between social network measure of three groups, along with their lower and upper 95% credible intervals in brackets. The mean synchrony from the three group pairings ( $r_{\text{avg}}$ ) is also presented to aid interpretation. Estimates of synchrony are provided for the model where sampling effort and shared events are accounted for (i.e. any remaining synchronization is likely to be due to extrinsic drivers). Synchrony estimates are also provided when accounting for season, and accounting for both season and NDVI (i.e. any remaining synchrony is likely to be due to other unidentified extrinsic drivers).

synchrony model	$r_{\text{PT,RBM}}$	$r_{\text{PT,RST}}$	$r_{\text{RBM,RST}}$	$r_{\text{avg}}$
<i>mean grooming strength</i>				
extrinsic drivers	0.68 (0.41,0.86)	0.55 (0.21,0.82)	0.65 (0.37,0.85)	0.63
accounting for season	0.68 (0.39,0.86)	0.61 (0.18,0.89)	0.63 (0.32,0.83)	0.64
accounting for season and NDVI	0.68 (0.42,0.86)	0.73 (0.46,0.89)	0.72 (0.47,0.88)	0.71
<i>grooming modularity</i>				
extrinsic drivers	0.58 (0.32,0.78)	0.16 (−0.24,0.50)	0.41 (0.06,0.68)	0.38
accounting for season	0.40 (0.06,0.68)	−0.20 (−0.54,0.19)	0.17 (−0.18,0.52)	0.12
accounting for season and NDVI	0.40 (0.05,0.66)	0.05 (−0.32,0.41)	0.38 (0.01,0.66)	0.28

groups, there was less synchrony in the kinds of social structure generated by this grooming behaviour. Contrary to prediction, however, there was a moderate amount of variability in synchronization, with the highest synchronization in grooming modularity between the RBM-PT groups ( $r_{\text{PT,RBM}} = 0.63$ ) and greatly reduced synchronization in their pairings with RST group ( $r_{\text{RBM,RST}} = 0.36$  and  $r_{\text{PT,RST}} = 0.08$ ). Given we have only estimated synchrony across three groups (i.e.  $n = 3$ ), this limits our ability to quantify this variation. Nevertheless, the three pairings showed a similar

decrease in synchronization (figure 3b) once the season was accounted for ( $r_{\text{avg}} = 0.12$ ), identifying this as a likely extrinsic driver of modularity dynamics. Grooming modularity reached its maximum values around day 180 (approx. June/July) in all groups (figure 4d), which falls near the end of the typical mating season in this population [48], and points to this as an important contributor to seasonal modularity dynamics. We also found that, when accounting for NDVI in the model, synchronization either remained the same or increased ( $r_{\text{avg}} = 0.28$ ), again confirming that while

groups were responding to NDVI, their responses were different. More specifically, NDVI had a negative impact on grooming modularity in two of the groups (RBM and PT), but little impact in RST (figure 4c). Once again, it is likely that the intrinsic characteristics of each group affect how grooming modularity changes with NDVI.

These results indicate that mean grooming strength is likely to be driven by extrinsic factors, although we cannot yet identify what these are. By contrast, beyond the influence of season, our results indicate that extrinsic factors are less likely to be driving grooming modularity. These results also point to an important distinction to be noted when interpreting the relative roles of extrinsic and intrinsic drivers from the estimated level of synchrony. That is, if synchrony is estimated to be 0.36, as for grooming modularity between RBM and RST, it is possible to conclude that extrinsic factors are responsible for *at least* 36% of the observed changes in modularity. Similarly, we can only conclude that intrinsic factors are responsible for *less than* the remaining 64%. This is due to potential interactions between intrinsic and extrinsic factors in the remaining variation, such as how the RBM group showed a decline in modularity with changes in NDVI, while RST did not. Highly synchronous patterns across social groups can therefore be used to identify extrinsic environmental factors as the primary drivers. Low synchrony outcomes, on the other hand, point only to either intrinsic, or intrinsic–extrinsic interactions as potential drivers.

Our results for mean grooming strength and grooming modularity were extracted using a single aggregation time scale of 60 days. However, these patterns might well change depending on the time scale chosen. Rather than identifying an optimal time scale for aggregation, it is possible that the way in which synchronization changes dependent on time scale will provide more insights [49]. For example, given the immediate consequences of social interactions within groups and the prolonged influence of the physical environment, one prediction might be that intrinsic factors might play more of a role at shorter time scales (low synchrony), and that extrinsic factors play more of a role (high synchrony) as time scales are increased. By estimating the magnitude of synchrony at multiple time scales, changes in synchrony could be compared across a range of species to gain insight into the speed at which environmental changes impact social structures.

The ability to apply the proposed network synchrony approach to distinguish between extrinsic and intrinsic drivers of social dynamics in other species/context will depend on the ability to have multiple social groups that share physical environmental conditions yet have distinctly separable social networks. In our case, female philopatry made this possible, while nevertheless requiring the

measurement of other sources of potential interactions between groups (e.g. number of ITEs and number of males in the group). Other species and landscape contexts, however, as well as captive or laboratory settings, might well provide useful opportunities to study more or less separable social systems, similar to studying population dynamics of goats on two nearby but separate islands [32].

From an epidemiological perspective, the ability to predict how social species will respond to environmental changes could facilitate better predictions of infectious disease spread. For our study population, our results suggest that extrinsic factors are a likely driver of the observed dynamics in the magnitude of host contact (mean grooming strength), while playing a smaller role influencing host social structures on which infectious diseases are transmitted (grooming modularity). By focusing on mean grooming strength and grooming modularity, it is possible to better understand the intrinsic/extrinsic drivers of a social network structure that are often linked to infectious disease transmission [8,36] and, thereby, provide insight into potential links between climate, social structure and infectious disease.

More generally, we suggest that focusing on intrinsic or extrinsic drivers separately can provide a misleading understanding of social network dynamics. Rather, to better understand their relative roles and interactions, patterns of synchronization in social network dynamics can identify and help guide future research in identifying, proximate mechanisms behind observed dynamics in social animal groups. Similarly, by using patterns of network synchronization to estimate the impacts of extrinsic drivers, it is possible to identify social species that might be more sensitive to landscape or climate changes.

**Data accessibility.** The code and the data used are available at [https://github.com/tbonne/network\\_synchrony](https://github.com/tbonne/network_synchrony).

Electronic supplementary material is available online [50].

**Authors' contributions.** T.R.B.: conceptualization, formal analysis, methodology, writing—original draft and writing—review and editing; S.P.H.: funding acquisition, resources, writing—original draft and writing—review and editing; L.B.: funding acquisition, resources, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We have no competing interests to declare.

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## References

1. Henzi S, Lusseau D, Weingrill T, Van Schaik C, Barrett L. 2009 Cyclicity in the structure of female baboon social networks. *Behav. Ecol. Sociobiol.* **63**, 1015–1021. (doi:10.1007/s00265-009-0720-y)
2. Bergman TJ, Beehner JC. 2015 Measuring social complexity. *Animal Behav.* **103**, 203–209.
3. Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234. (doi:10.1126/science.1088580)
4. McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet TV, Barrett L. 2017 The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. *Anim. Behav.* **126**, 101–106. (doi:10.1016/j.anbehav.2017.02.002)
5. Alberts SC. 2019 Social influences on survival and reproduction: insights from a long-term study of wild baboons. *J. Anim. Ecol.* **88**, 47–66. (doi:10.1111/1365-2656.12887)

6. Snyder-Mackler N *et al.* 2020 Social determinants of health and survival in humans and other animals. *Science* **368**, aax9553. (doi:10.1126/science.aax9553)
7. Josephs N, Bonnell T, Dostie M, Barrett L, Henzi SP. 2016 Working the crowd: sociable vervets benefit by reducing exposure to risk. *Behav. Ecol.* **27**, 988–994.
8. Nunn CL, Jordán F, McCabe CM, Verdolin JL, Fewell JH. 2015 Infectious disease and group size: more than just a numbers game. *Phil. Trans. R. Soc. B* **370**, 20140111. (doi:10.1098/rstb.2014.0111)
9. McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015 Social integration confers thermal benefits in a gregarious primate. *J. Anim. Ecol.* **84**, 871–878. (doi:10.1111/1365-2656.12329)
10. Croft DP, James R, Krause J. 2008 *Exploring animal social networks*. Princeton, NJ: Princeton University Press.
11. Whitehead H. 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.
12. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)
13. Brent LJ, MacLarnon A, Platt ML, Semple S. 2013 Seasonal changes in the structure of rhesus macaque social networks. *Behav. Ecol. Sociobiol.* **67**, 349–359. (doi:10.1007/s00265-012-1455-8)
14. Aplin LM *et al.* 2015 Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Anim. Behav.* **108**, 117–127. (doi:10.1016/j.anbehav.2015.07.016)
15. Ilany A, Akçay E. 2016 Social inheritance can explain the structure of animal social networks. *Nat. Commun.* **7**, 12084. (doi:10.1038/ncomms12084)
16. O'Brien PP, Webber QMR, Vander Wal E. 2018 Consistent individual differences and population plasticity in network-derived sociality: an experimental manipulation of density in a gregarious ungulate. *PLoS ONE* **13**, e0193425. (doi:10.1371/journal.pone.0193425)
17. Pinter-Wollman N *et al.* 2014 The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255. (doi:10.1093/beheco/art047)
18. Formica VA, Wood C, Brodie III E. 2017 Consistency of animal social networks after disturbance. *Behav. Ecol.* **28**, 85. (doi:10.1093/beheco/arw128)
19. Piefke TJ, Bonnell TR, DeOliveira GM, Border SE, Dijkstra PD. 2021 Social network stability is impacted by removing a dominant male in replicate dominance hierarchies of a cichlid fish. *Anim. Behav.* **175**, 7–20. (doi:10.1016/j.anbehav.2021.02.012)
20. Snijders TA, Van de Bunt GG, Steglich CE. 2010 Introduction to stochastic actor-based models for network dynamics. *Soc. Netw.* **32**, 44–60. (doi:10.1016/j.socnet.2009.02.004)
21. Fisher DN, Ilany A, Silk MJ, Tregenza T. 2017 Analysing animal social network dynamics: the potential of stochastic actor-oriented models. *J. Anim. Ecol.* **86**, 202–212. (doi:10.1111/1365-2656.12630)
22. Barrett L, Henzi SP, Lusseau D. 2012 Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Phil. Trans. R. Soc. B* **367**, 2108–2118. (doi:10.1098/rstb.2012.0113)
23. Dickison ME, Magnani M, Rossi L. 2016 *Multilayer social networks*. Cambridge, UK: Cambridge University Press.
24. Finn KR, Silk MJ, Porter MA, Pinter-Wollman N. 2019 The use of multilayer network analysis in animal behaviour. *Anim. Behav.* **149**, 7–22. (doi:10.1016/j.anbehav.2018.12.016)
25. Bonnell TR, Vilette C, Young C, Henzi SP, Barrett L. 2020 Formidable females redux: male social integration into female networks and the value of dynamic multilayer networks. *Curr. Zool.* **67**, 49–57. (doi:10.1093/cz/zoaa041)
26. Cross PC, Lloyd-Smith JO, Bowers JA, Hay CT, Hofmeyr M, Getz WM. 2004 Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici* **2004**, 879–892.
27. Wittemyer G, Douglas-Hamilton I, Getz WM. 2005 The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.* **69**, 1357–1371. (doi:10.1016/j.anbehav.2004.08.018)
28. de Silva S, Ranjewa ADG, Kryazhimskiy S. 2011 The dynamics of social networks among female Asian elephants. *BMC Ecol.* **11**, 17. (doi:10.1186/1472-6785-11-17)
29. Godfrey SS, Sih A, Bull CM. 2013 The response of a sleepy lizard social network to altered ecological conditions. *Anim. Behav.* **86**, 763–772. (doi:10.1016/j.anbehav.2013.07.016)
30. Ilany A, Booms AS, Holekamp KE. 2015 Topological effects of network structure on long-term social network dynamics in a wild mammal. *Ecol. Lett.* **18**, 687–695. (doi:10.1111/ele.12447)
31. Smith-Aguilar SE, Ramos-Fernández G, Getz WM. 2016 Seasonal changes in socio-spatial structure in a group of free-living spider monkeys (*Ateles geoffroyi*). *PLoS ONE* **11**, e0157228. (doi:10.1371/journal.pone.0157228)
32. Grenfell B, Wilson K, Finkenstädt B, Coulson T, Murray S, Albon S, Pemberton J, Clutton-Brock T, Crawley M. 1998 Noise and determinism in synchronized sheep dynamics. *Nature* **394**, 674–677. (doi:10.1038/29291)
33. Hilfinger A, Paulsson J. 2011 Separating intrinsic from extrinsic fluctuations in dynamic biological systems. *Proc. Natl Acad. Sci. USA* **108**, 12 167–12 172. (doi:10.1073/pnas.1018832108)
34. Levins R, Lewontin R. 1985 *The dialectical biologist*. Cambridge, MA: Harvard University Press.
35. Cantor M *et al.* 2021 The importance of individual-to-society feedbacks in animal ecology and evolution. *J. Anim. Ecol.* **90**, 27–44. (doi:10.1111/1365-2656.13336)
36. Griffin RH, Nunn CL. 2012 Community structure and the spread of infectious disease in primate social networks. *Evol. Ecol.* **26**, 779–800. (doi:10.1007/s10682-011-9526-2)
37. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. (doi:10.1163/156853974X00534)
38. Blerch R, Bonnell TR, Ganswindt A, Young C, Barrett L, Henzi SP. 2021 Sick and tired: sickness behaviour, polyparasitism and food stress in a gregarious mammal. *Behav. Ecol. Sociobiol.* **75**, 1–15. (doi:10.1007/s00265-021-03111-3)
39. Pasternak G, Brown LR, Kienzle S, Fuller A, Barrett L, Henzi SP. 2013 Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe* **55**, 1–9. (doi:10.4102/koedoe.v55i1.1078)
40. Bonnell TR, Vilette C. 2020 Constructing and analysing time-aggregated networks: the role of bootstrapping, permutation and simulation. *Methods Ecol. Evol.* **12**, 114–126. (doi:10.1111/2041-210x.13351)
41. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
42. Csardi G, Nepusz T. 2006 The igraph software package for complex network research. *InterJournal Complex Systems* **1695**, 1–9.
43. Young C, McFarland R, Ganswindt A, Young MM, Barrett L, Henzi SP. 2019 Male residency and dispersal triggers in a seasonal breeder with influential females. *Anim. Behav.* **154**, 29–37. (doi:10.1016/j.anbehav.2019.06.010)
44. Pearl J, Mackenzie D. 2018 *The book of why: the new science of cause and effect*. New York, NY: Basic Books.
45. McElreath R. 2020 *Statistical rethinking: a Bayesian course with examples in R and Stan*. Boca Raton, FL: CRC press.
46. Young C, Bonnell TR, Brown LR, Dostie MJ, Ganswindt A, Kienzle S, McFarland R, Henzi SP, Barrett L. 2019 Climate induced stress and mortality in vervet monkeys. *R. Soc. Open Sci.* **6**, 191078. (doi:10.1098/rsos.191078)
47. Bürkner PC. 2017 brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28. (doi:10.18637/jss.v080.i01)
48. McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP. 2014 Behavioral flexibility of vervet monkeys in response to climatic and social variability. *Am. J. Phys. Anthropol.* **154**, 357–364. (doi:10.1002/ajpa.22518)
49. Levin SA. 1992 The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967. (doi:10.2307/1941447)
50. Bonnell TR, Henzi SP, Barrett L. 2022 Using network synchrony to identify drivers of social dynamics. Figshare. (doi:10.6084/m9.figshare.c.6049199)