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ORIGINAL ARTICLE

Network reaction norms: taking account of network position and plasticity in response to environmental change

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Abstract

Consistent inter-individual differences in behaviour are thought to be related to consistency in social network position. There is also evidence that network structures can show predictable temporal dynamics, suggesting that consistency in social network position across time does not preclude some form of plasticity in response to environmental variation. To better consider variation in network position and plasticity simultaneously, we investigate the extension of the behavioural reaction norm (BRN) to dynamic social networks. Our aim is to estimate both an individual's position and plasticity within a network across an environmental gradient (i.e. to generate a network reaction norm (NRN)). We show that it is possible to account for the non-independence of network measures using covariance structures but that, in cases where the independent variables are group-level environmental measures, a standard multilevel model is sufficient. We therefore outline when a standard multilevel model is appropriate for NRNs and highlight the benefits and limitations to this approach. As an illustrative example, we used an NRN approach on 7 years of behavioural data on chacma baboons to quantify both the consistency with which individuals maintained social behaviour (node strength) and central positions (eigenvector centrality) within the social network. We found evidence for individual plasticity for node strength but little evidence for eigenvector centrality. Conversely, we found evidence of consistent individual differences in eigenvector centrality but not strength. These results suggest that individual node strengths are influenced by environmental changes, but the social structure of the group remains remarkably stable nevertheless. We suggest that expanding from measures of repeatability in social networks to network reaction norms will provide a more contextually nuanced way to investigate social phenotypes, leading to a better understanding of the development and maintenance of social structures in changing environments.

Significance statement

An individual's position within a social network can have consequences for its fitness, resulting in great interest into how individuals develop and maintain particular network positions. Here, we extend the notion of behavioural reaction norms to include social network data. Given the non-independence of network data, however, the application of BRNs is not straightforward. Consequently, we have developed an alternative statistical extension that uses covariance structures to account for non-independence. Although we find that under one specific set of assumptions, it is possible to apply the standard BRN to network data. Applying this approach to data from a social group of chacma baboons, we found individual social behaviours shifted in response to environmental variables, yet the social structure of the group remained remarkably stable.

Keywords Dynamic social networks · Behavioural reaction norm · Network plasticity · Repeatability · Chacma baboon

Introduction

Consistent inter-individual differences in behaviour are common in animal groups (Sih et al. 2004; Dall et al. 2012). How such behavioural differences develop, are maintained, and selected form the focus of current research efforts, as do questions relating to the ecological and evolutionary consequences of such inter-individual differences (Wolf and

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Weissing 2012; Bierbach et al. 2017; Jolles et al. 2020). There is also great interest in the extent to which animals are able to vary their behaviour in response to environmental changes, and whether and how this behavioural plasticity covaries with inter-individual differences in mean behavioural rates. These behavioural patterns are captured by the notion of a "behavioural reaction norm" (BRN)—the set of behavioural phenotypes an individual produces in a given set of environments—a concept drawn from life history theory (Dingemanse et al. 2010; Westneat et al. 2015).

Within social groups, patterns of inter-individual consistency have also been observed in social network position (e.g. central individuals remain central across time) (Brent et al. 2013; Aplin et al. 2015; Formica et al. 2017; Krause et al. 2017; Blaszczyk 2018; O'Brien et al. 2018). It is an open question as to how these differences arise and are maintained (Firth et al. 2017). There is also evidence to suggest that consistent inter-individual differences in behaviour and social network position covary (Croft et al. 2009; Aplin et al. 2013). For social animals, this implies that network position reflects certain behavioural predispositions, and/or that certain behavioural predispositions may arise in response to occupying a particular network position.

At the same time, there are data showing that the network structure itself exhibits strong temporal dynamics. Furthermore, temporal consistency in social network position does not preclude some form of plasticity in response to environmental variation, such that network position and plasticity may covary in interesting ways (Henzi et al. 2009). Such covariation could provide insight into the possible constraints or opportunities faced by group-living individuals. For example, we might find covariation if individuals occupying more central positions in the network are better (or less) able to cope with environmental changes in ways that are not available to others. Examining the covariation between node position and plasticity may act as a guide to the discovery of the mechanisms that produce social network structures, as well as their functional consequences.

Currently, repeatability measures are used to quantify the variation in individual network positions through time (Wilson et al. 2013; Jacoby et al. 2014; Aplin et al. 2015; Formica et al. 2017; O'Brien et al. 2018), for example, do some individuals consistently have low/high node eigenvector centrality values. In statistical terms, the measure of repeatability estimates the proportion of variation that can be attributed to between-subject variation (Nakagawa and Schielzeth 2010). If individuals have consistently different network positions, this measure will be high, whereas if individuals hold similar positions, or swap positions frequently, then the measure of repeatability will be low. Quantifying the pattern of repeatability in social networks has allowed for useful comparisons between and within social groups and has also been useful in testing and identifying potential processes that underlie observed social dynamics (Firth et al. 2017). We suggest that we can build on the insights gained from studies of repeatability (i.e. consistent inter-individual differences) by extending our investigations to consider node plasticity across different environmental conditions (O'Brien et al. 2018). Within the behavioural ecology literature it has been productive, and in some cases essential, to consider both inter-individual differences in mean behavioural traits and individual differences in behavioural plasticity (Westneat et al. 2011, 2015; Dingemanse and Wolf 2013). We suggest that considering both network position and plasticity of nodes will be similarly useful for quantifying patterns of dynamic social networks.

We therefore consider whether a behavioural reaction norm approach (Dingemanse et al. 2010) can be used to model inter- and within-individual changes in social network position—a "network reaction norm" (NRN)—and use this to quantify individual variation in social phenotypes. As the applications of reaction norms to social networks raise some interesting analytical and conceptual challenges (specifically, the non-independence of nodes), we also apply this approach to a simulated dataset to determine what it can and cannot achieve. We then apply the NRN framework to a network of wild baboons as a proof-of-concept and address the question of whether individuals maintain similar network positions in response to changes in both rainfall and solar radiation.

Methods

Network reaction norm

Behavioural reaction norms are calculated using a multilevel modelling approach where, for each individual, grouping terms are used to calculate both their deviation from the overall mean behaviour (random intercept) and the change seen in behaviour in response to a change in the environment (i.e. random slope). With network data, however, as node measures within a network are not independent (i.e. the value of a network measure for one node is intrinsically linked to the values of network measures of other nodes in the network), this limits the ability to use routine BRN models. The non-independence of network data can bias estimates from a statistical model, such as a BRN, as well as the uncertainty around these estimates (Croft et al. 2011; Farine 2017). We can, however, build on the BRN approach to account for the non-independence of nodes by using a multivariate multilevel normal distribution (MVN).

$$y_{i,t} \sim MVN\left(\mu_{i,t}, \Sigma\right)$$

where $y_{i,t}$ is the node measure for the i^{th} node at time t, $\mu_{i,t}$ is the mean for node i at time t, and Σ is a covariance matrix describing the dependence between nodes:

$$\Sigma = \begin{pmatrix} p_{1,1} & \cdots & p_{1,n} \\ \vdots & \ddots & \vdots \\ p_{n,1} & \cdots & p_{n,n} \end{pmatrix}$$

Here, $p_{1,2}$, for example, is the covariance in the errors between nodes 1 and 2, and n is the total number of nodes. If the node measures in NRNs are repeated measures of individual nodes across different environments over time (i.e. over an environmental gradient), it is then possible to introduce node intercepts and slopes following the traditional multilevel model structure used in BRN approaches:

$$\mu_{i,t} = a + a_i + (b + b_i) * x_t$$

where a is the mean intercept shared across all nodes, a_i is the deviation of the i^{th} node from the mean intercept, and b is the mean slope shared across all nodes, with b_i being the deviation of the i^{th} node from the mean slope, and x_t is an environmental measure at time t. Using this approach, an NRN can be seen as a multivariate approach to a traditional BRN.

Avoiding statistical confounding in NRNs

The use of a multivariate distribution in the NRN approach allows us to account for covariance structures in node measures. That is, a covariance structure captures the dependencies between node measures (e.g. how some nodes might increase in eigenvector centrality resulting in other nodes decreasing in eigenvector centrality). However, there remains the potential for statistical confounding when predictor variables also have covariance structures (i.e. another network measure) or are influenced by the covariance structure of the outcome variable (e.g. individual-level phenotypes).

To give an example, problems of statistical confounding would likely arise if we wanted to know if body size predicts the number of unique partners (represented by the network centrality measure *degree*). In this example, we know that degree is a network measure and that it will have some covariance structure. In this system, it might also be a reasonable assumption that network position might influence the body size of individuals. As a result, both degree and body size are likely influenced by the same network covariance. If not accounted for, this can lead to statistical confounding, where an estimate of *body size* on *degree* might be misleading if the covariance structure of the network is not taken into account (Krackhardt 1988).

When building a statistical model with a response and predictor variable that potentially share similar covariance patterns, permutation approaches have been suggested as a means of breaking this shared covariance (Krackhardt 1988; Weiss et al. 2021; Farine and Carter 2022). However, the use of permutations with regression models can lead to undesirable statistical properties (Weiss et al. 2021). Crucially, in cases where the predictor variable is an environmental measure that is the same for all nodes in a social network (e.g. rainfall), there is no associated covariance structure, and so there is no need for permutations. We provide a graphical approach (Pearl and Mackenzie 2018) to help visualise when an NRN can and cannot be applied with non-environmental measures (Fig. 1). In the rest of the paper, we focus on NRNs where the independent variable is a physical environmental variable that can safely be assumed not to have any shared covariance with node measures.

Case 1: If the network structure of a group influences the predictor variable x, then x cannot be included in an NRN due to potential statistical confounding (Fig. 1a). In our study presented here, as x is a measure of an environmental variable that influences the entire group, such as rainfall, or temperature, the social structure of a group is unlikely to impact these large-scale environmental measures. Case 2: If a third variable influences both the network structure and the predictor variable x, then x cannot be included in an NRN unless the third variable can be included in the model as well, e.g. if rainfall influences both network structure and humidity, then rainfall would need to be included in the NRN to get an unbiased estimate of humidity on network structure (Fig. 1b). Case 3: If the reverse is true, that both network structure and the independent variable x influences some third variable, an NRN can be run as long as that third variable is not included (Fig. 1c). This is another case that is unlikely to occur with NRNs as social structures would be required to influence large-scale environmental measures. Case 4: Finally, if the independent variable x influences network structure, but cannot be influenced by the network structure (Fig. 1d), then it is possible to estimate the total effect of the independent variable x on an individual's network measure. This last assumption can be safely assumed with many large-scale environmental measures, such as temperature, rainfall, or solar radiation.

Simulation data

To better understand the limits and opportunities of using a reaction norm approach with social network measures, we make use of a simple social network simulation to generate some test data. We present a social context where there are two clusters of individuals connected by a single dyadic relationship (Fig. 2). Furthermore, this between-cluster relationship is made dependent on food availability, where the relationship increases with increased food availability. We then vary food availability and measure an indirect network

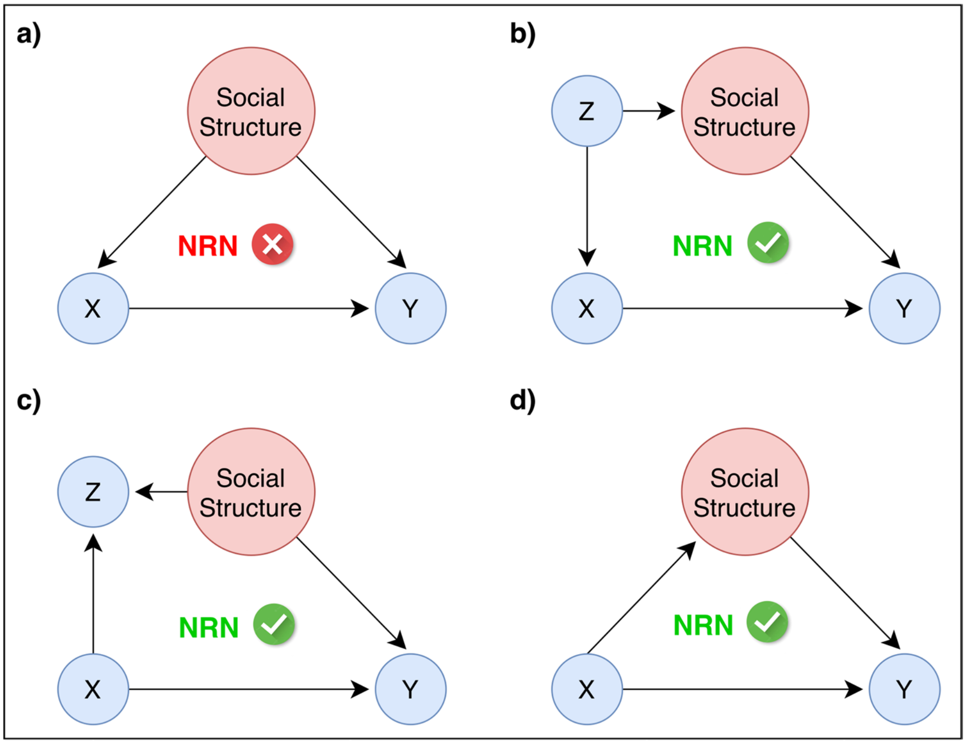

Fig. 1 Outlining different cases where the NRN (network reaction norm) approach can/cannot be run without the presence of statistical confounding. In each case, a different assumption of the relationship between the independent variable *x* (e.g. rainfall), dependent network measure *y* (e.g. node strength), and the social structure of a social group is made: **a** social structure influences the independent variable *x*, **b** a third variable *z* influences both the social structure as well as *x*, **c** a third variable *z* is influenced both by *x* and social structure, and **d** *x* influences the social structure. The ability to fit an NRN is highlighted in green with a checkmark, and in the case where it cannot, in red with an *x*-mark

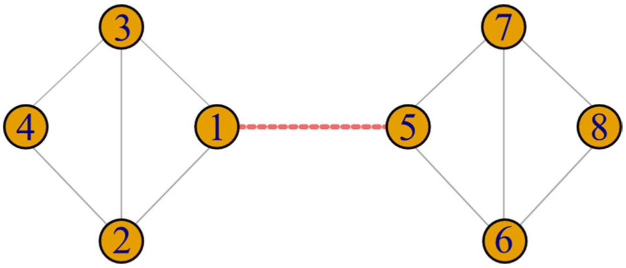

Fig. 2 Two cluster network used to simulate data for a test case of the network reaction norm approach. The grey edges are fixed, while the red dashed edge is made dependent on the availability of food

measure—node eigenvector centrality (i.e. one where the individual's measure is dependent on all other individuals within the network)—and a direct network measure—node strength (i.e. where individual measures are only dependent on neighbouring nodes). A simplistic simulation of two clusters connected by one edge was chosen to offer a clear case of the benefits and limits of the NRN approach and how it can be used and interpreted under more realistic conditions.

Observed data

To investigate how social network structure changes with varying environmental conditions in a wild population, we used proximity data collected between June 1997 and October 2006 from all adult females of a troop of baboons in the De Hoop Nature Reserve, South Africa (Barrett et al. 2002; Henzi et al. 2009). Data were collected by scan sampling every 30 min, during which the identities of all animals within 10 m of the target individual were recorded (hereafter nearest neighbours) for a total of 25,806 nearest neighbour events across the study period. The final dataset consisted of 30 females, where the median number of females at any given time was 12 (min = 9, max = 16) over the entire study period. It was not possible to record data blind because our study involved focal animals in the field.

To gain an understanding of how social network structures vary with changing environments, we generated a sequence of time-aggregated networks. To accomplish this, we make use of a moving window design, where a window of a fixed duration shifts by a set amount of time, generating a time series of networks (Bonnell and Vilette 2021). In selecting the temporal scale, we used a window size of 3 months, and a shift of 3 months, to avoid window overlap. We chose this 3-month time scale given the results from using a bootstrapping and subsampling approach to identify the lower limit to possible time scale choices. These results suggested that below 1 month, our network measures showed high sensitivity to the bootstrapped sample; hence, > 30-day windows would be required. Similarly, we varied window size to look for natural scales (Caceres et al. 2011). When we measured the amount of structure in the resulting time series, the results suggested that the 3-month window size represented a transition from highly noisy time series to more structured time series. Both of these methods are discussed in greater detail in Bonnell and Vilette (2021), and the results are presented in the supplementary material (Fig. S2, S3, S4). The chosen time scale of 3-month windows resulted in a mean observation time within windows of 178 h.

To ensure that the network measures were robust throughout the duration of the study, we excluded networks constructed using fewer than 50 h of data collection, and where the lower 95% credible interval of the cosine similarity between the observed network measures and network measures generated from bootstrapped samples was below 0.90.

Using this time series of networks, we extracted individual measures of strength and eigenvector centrality (EC) (Newman 2018), producing a time series of network measures for each individual. Individual node strength represents the number of times an individual was found within 10 m of another individual, whereas EC assesses the centrality of each node based on their direct and indirect connections to others. So, for example, in a fully connected network, all nodes receive equal centrality scores, whereas at the other extreme, a network where all dyadic ties involve one particular individual (e.g. a star network) will result in this individual receiving the highest centrality score. More generally, the use of centrality measures that take into account indirect connections has proven useful in better understanding the fitness and heritable nature of network positions within social groups (Brent et al. 2013; Brent 2015; Wice and Saltz 2021). Finally, we removed individual measures of strength and EC that extrapolated beyond the range where individuals were observed, e.g. if individual A had an eigenvector measure of 0.2 for the window covering days 0–100, but was first observed on day 50, and died on day 200, this measure was removed.

A more detailed walkthrough of the steps taken with the observed data is available with the code and data provided online (https://github.com/tbonne/NRN), as well as in the supplementary sections (Supplementary material, workflow example).

Quantifying the changing physical environment

To estimate how individuals responded to environmental changes, we used two ecological variables. We used mean incoming solar radiation over each time window, measured as Watts/m^2, as an environmental effect with the potential for impact on thermoregulatory behaviour (Sevi et al. 2001; Amat and Masero 2004; Tucker et al. 2008). Estimates of surface solar radiation for our study site and study period were acquired from the Heliosat dataset, which uses the Heliosat algorithm and geostationary satellites to estimate solar surface irradiance at a spatial resolution of $0.05° \times 0.05°$ (Müller et al. 2015). We used mean rainfall within each window as an index of the amount of available food at the site (Barrett et al. 2006; McFarland et al. 2014). These two environmental measures showed a low but uncertain correlation ($r = -0.11$; 95% credible interval (CI): -0.43, 0.23).

Statistical analysis

Using the simulated data, we fit an NRN to both strength and eigenvector centrality (Table S1). Crucially, as the use of covariance structure with Gaussian multivariate models results in analytical difficulties when datasets contain missing data, or nodes enter/leave the network, we also use the simulated data to highlight the implications of using NRNs without covariance structures. To do so, we first test the approach of running multiple univariate models that use a multilevel modelling approach to pool information across models to estimate intercepts and slopes within each model (Table S2). We then test the approach of running a standard multilevel model (i.e. random intercept-slope model), with the inclusion of a random intercept for the standard deviation using ID as the grouping term (Table S3). The standard multilevel model approach has the advantage that it can be easily run in R using the brms package, e.g. bf(node_strength ~ food + (1 + food|nodeID), sigma ~ 1 + (1|nodeID), family = gaussian) (see supp. workflow example). We then compare these two approaches to the slopes and intercepts estimated in the Gaussian multivariate multilevel model, comparing both the mean and standard deviation of the estimates.

Given the results of the simulation, we then fit NRNs using the standard multilevel modelling approach on the observed dataset for both strength and eigenvector centrality measures. For strength, we modelled the rate of observed spatial proximity events by dividing the observed count by the amount of observation time. To account for potential sampling bias, e.g. the possibility that some individuals were sampled only in high rainfall conditions, we included the mean environmental conditions experienced by each individual in the NRN. By including this mean environmental condition, we were able to partition within- and between-individual effects of the environment (van de Pol and Wright 2009). For each environmental variable (i.e. rain and solar radiation), we used linear terms and allowed all individuals to vary in their response to environmental changes by including random intercept and slope terms, using ID as the grouping variable. We also included a non-linear seasonal effect by including a circular regression spline on the day of the year. Finally, we accounted for autocorrelation in the residuals using an AR(1) process (Dutilleul 2011). We used the R package “brms” (Bürkner 2017) to fit the model in a Bayesian framework. We scaled and centred our dependent and independent variables, and used weakly informative priors centred on zero, i.e. Normal(0,1). Using these priors means that we started our models under the assumption that the environmental variables are most likely to have no effect (McElreath 2020). Model diagnostics suggest MCMC convergence, with all $\hat{R} < 1.01$ and effective sample sizes > 300. All analyses were run in the R programming environment 3.5.2.

Results

Simulated data: NRN with covariance

Fitting an NRN to node strength, using a Gaussian multilevel multivariate model, accurately finds that only two nodes (1, 5) show plasticity in response to changes in food availability and that there are inter-individual differences in intercepts (Fig. 3a). In the case of node EC, we see that plasticity in one relationship impacts all nodes; that is, all nodes show plasticity in relation to changes in food availability (Fig. 3b). We also found that the covariance structure estimated in the model using the indirect network measure (i.e. EC) closely matches the underlying network used in the simulation (Figs. 2 and 3d). In the case of the local measure (i.e. strength), the model correctly found little evidence of covariance in measure errors (Fig. 3c).

Comparing the direct and indirect NRN shows how using reaction norms, at different scales and different measures, can provide insight into the response of social networks to changes in the environment. Here, we can see that in the node strength NRN, some nodes are correctly estimated to show no plasticity (e.g. Figure 2a nodes 4 and 8), while still showing plasticity in the model with the indirect measure (i.e. EC) (e.g. Figure 2b nodes 4 and 8). The contrast between direct and indirect measures correctly suggests that the resulting plasticity observed in their indirect network measure is due to the behaviour of others (i.e. other relationships changing that are not directly linked to the individual in question).

Simulated data: NRN without covariance

When we drop the covariance matrix, and NRNs were fit using the multiple univariate model approach, as well as the standard multilevel modelling approach, mean estimates of the intercepts and slopes did not show bias (Fig. 4, S5). We did, however, find that the estimated standard deviations of the estimated intercepts and slopes were biased slightly higher in the model using multiple univariate models, but not with the standard multilevel modelling approach (Fig. S5).

Observed data results

The results of the baboon NRN on node strength suggest some plasticity within the population to both solar radiation and rainfall. The population shows an increase in node strength (i.e. proximity events) with increased rainfall ($b_{\text{rain}} = 0.16$ (95% CI: 0.06, 0.27) and decreased solar radiation ($b_{\text{solar}} = -0.11$ (95% CI: −0.22, 0.00) (Table 1). There was also little evidence for both individual differences in slopes or intercepts in the population (*sd* parameters Table 1). Conversely, in the case of eigenvector centrality, the NRN suggested little population-level plasticity in response to environmental change ($b_{\text{rain}} = 0.02$ (95% CI: −0.07, 0.11), $b_{\text{solar}} = -0.07$ (95% CI: −0.16, 0.02), Table 1). There was, however, evidence for individual differences in intercepts ($\text{sd}_{\text{intercept}} = 0.38$, 95% CI: 0.15, 0.64) and some evidence of individual differences in response to solar radiation but not rainfall ($\text{sd}_{\text{rain}} = 0.05$, 95% CI: 0.00,

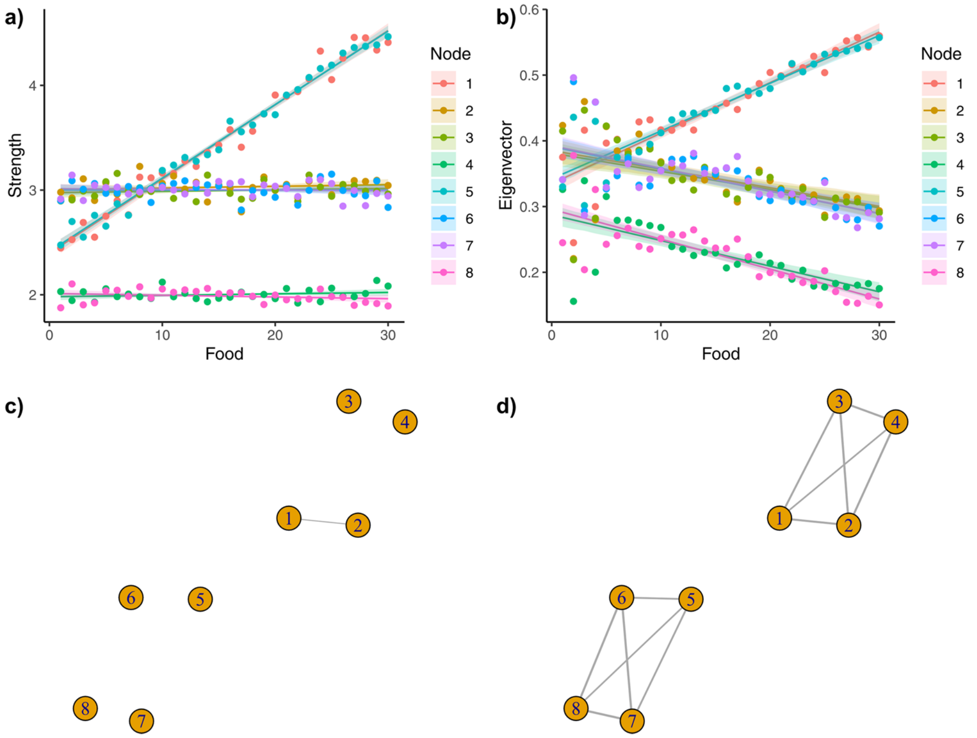

Fig. 3 Network reaction norms applied to the simulated example. As these are simulated data, where we know how precisely how the data were generated, we show in **a** that estimated changes in mean strength in response to food availability only go up for nodes 1 and 5. In **b**, we show that changes in mean eigenvector for each node in response to food availability changes for all nodes (i.e. indirect effects). While in **c** and **d,** we show that using a multivariate approach helps us to correctly estimate the correlation matrix of the errors for **c** node strength measures and **d** eigenvector centrality measures. By presenting this matrix in a network format, each edge represents a correlation between errors (i.e. edges show where unexplained changes in eigenvector centrality are correlated between nodes)

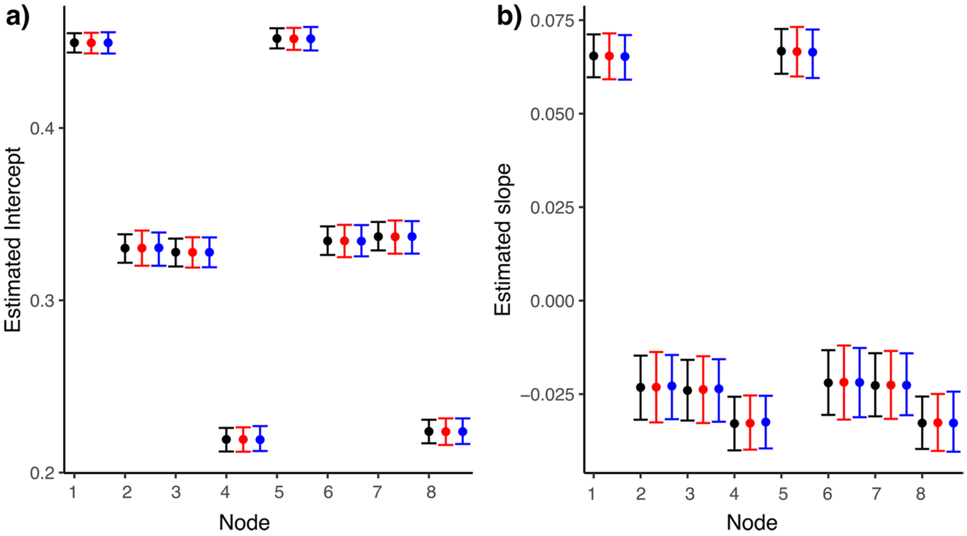

Fig. 4 Comparing estimates of how individual eigenvector centrality changes in response to food using three different statistical approaches. The black points are estimates from a multilevel multivariate normal distribution model that estimates the covariance between nodes, while the red points are from a model using the multiple univariate model approach without estimating covariance between nodes. Finally, the blue points are estimates from the standard multilevel model. The estimates in **a** are the estimated node intercepts, while estimates in **b** are the estimated slopes describing how node's eigenvector centrality responds to food. The 95% credible intervals are provided as error bars around the points. These models were all fit to simulated data

0.15; $sd_{solar} = 0.08$, 95% CI: 0.00, 0.21). The eigenvector centrality model also suggests that the individual differences found were not correlated. For example, the correlation between individual differences in mean eigenvector centrality and individual differences in response to solar radiation was − 0.14 (95% CI: 0. − 79, 0.87) (see Table 1 for all correlation results).

Taken together, these patterns can be seen in an NRN plot where each line represents the estimated response of each individual in the population to changes in the environment (Fig. 5). We can see the plastic response of individual strength to solar radiation and rainfall, with few consistent differences between individuals (Fig. 5a, b). In the case of individual eigenvector centrality values, we find the opposite. Namely, individuals show mean differences in eigenvector centrality, and some individuals show individual differences in response to solar radiation, resulting in the ordering of which individuals are most central being dependent on environmental conditions (Fig. 5c, d).

Discussion

Overall, our results suggest that it is possible to use an NRN approach to quantify how networks change in response to variation in the environment, both in terms of node positions and plasticity. We found that it is possible to account for the non-independence of node measures by using a multivariate approach that can estimate a covariance matrix describing the dependence between nodes. The use of covariance matrices in applied settings, however, can be complicated when there are missing data, or when network composition is dynamic. In these cases, we have found that standard multilevel models without covariance structures also provide accurate estimates. Related to this result, we suggest the problem of statistical confounds due to shared covariance structures between predictors and response variables is circumvented when using group-level environmental measures as predictors—e.g. daily temperature/rainfall. In the context of quantifying how social structures change in response to climate or landscape changes, this suggests that NRNs are likely to be widely applicable.

Our finding that multilevel models are suitable for modelling network data fits into the wider discussions about the use of permutations versus model-based approaches (Hart et al. 2021; Weiss et al. 2021; Farine and Carter 2022). In general, permutation approaches have been advocated as essential for dealing with potential confounds in network data. We have shown here that the use of covariance matrices can be another useful tool to account for, and estimate, the non-independence of the data. The estimation of these covariation matrices can, in and of themselves, also provide useful insights (Fig. 3c, d). Similarly, a more nuanced recognition of when confounding is a problem can provide guidance when standard multilevel models are appropriate

Table 1 Parameter estimates for the network reaction norm (NRN) of strength and eigenvector centrality. We present the parameter estimates of the model partitioned into (1) the population-level effects containing the mean responses, (2) the magnitude of individual differences in responses, (3) the correlation between individual differences, and (4) the estimated effect size using *r*-squared. The autocorrelation term ar[1] is the estimated magnitude of the autoregressive process of order 1. For each parameter, the 95% lower/upper credible intervals are presented. Solar radiation is referred to in the table as SIS

NRN	Category	Parameter	Mean	Lower CI	Upper CI
Strength	Population	Rain	0.16	0.06	0.27
		Rain (between)	0.81	0.05	1.59
		SIS	−0.11	−0.22	0.00
		SIS (between)	1.01	0.20	1.79
	Individual differences	sd(Intercept)	0.15	0.01	0.39
		sd(SIS)	0.08	0.00	0.22
		sd(Rain)	0.07	0.00	0.20
		sd(Sigma)	0.24	0.04	0.46
	Correlations	cor(Inter,SIS)	−0.06	−0.91	0.86
		cor(Inter,Rain)	−0.03	−0.89	0.86
		cor(SIS,Rain)	−0.09	−0.91	0.86
		ar[1]	0.40	0.27	0.53
	Effect size	Marginal R^2	0.12	0.05	0.21
		Conditional R^2	0.16	0.07	0.26
Eigenvector	Population	Rain (within)	0.02	−0.07	0.11
		Rain (between)	0.27	−0.70	1.22
		SIS (within)	−0.07	−0.16	0.02
		SIS (between)	1.17	−0.03	2.36
	Individual differences	sd(Intercept)	0.38	0.15	0.64
		sd(SIS)	0.08	0.00	0.21
		sd(Rain)	0.05	0.00	0.15
		sd(Sigma)	0.25	0.13	0.40
	Correlations	cor(Inter,SIS)	0.14	−0.79	0.87
		cor(Inter,Rain)	−0.20	−0.93	0.79
		cor(SIS,Rain)	−0.04	−0.88	0.87
		ar[1]	0.48	0.37	0.60
	Effect size	Marginal R^2	0.04	0.01	0.11
		Conditional R^2	0.19	0.07	0.31

(Fig. 1). We take advantage of this more nuanced understanding of confounding in social network data to show that the standard multilevel modelling approach can be used as an NRN when estimating the impacts of environmental variables on social network position and plasticity. Additionally, there have been recent advancements in the use of a multilevel modelling that can better account for some of the uncertainty in network measures themselves, which could complement or replace the time aggregation approach used in this paper (Hart et al. 2022; Ross et al. 2022).

Using the NRN approach with our study population of chacma baboons, individuals showed similar plastic responses to environmental changes in terms of their network strength (i.e. the number of times an individual was seen in close proximity to another individual) (Fig. 5a, b). Despite these changes in social behaviour, however, individual eigenvector centrality within the overall network remained relatively stable (Fig. 5c, d). That is, there were consistent individual differences in mean network positions, where some individuals were, on average, consistently higher in eigenvector centrality than others. We did find some evidence that changes in solar radiation could impact the order of who was most central, and reduce mean individual centrality, but the most striking trend was that of a stable global network structure in response to environmental changes. This suggests that, in this population, individual network positions are maintained despite changes to individual social behaviours. Additionally, we found that across both node strength and eigenvector centrality, a comparison of differences in mean network position and plasticity in response to environmental change showed very little correlation (i.e. more central individuals did not show increased/decreased plasticity in response to environmental change compared to less central individuals).

Biologically speaking, maintenance of a stable network structure in the face of changing social behaviour has some interesting implications. In terms of directly transmitted diseases, for example, our results suggest that individuals that are found consistently in central positions could be at higher risk of infection and could be efficient vectors of disease spread to others (Romano et al. 2016). In addition, the

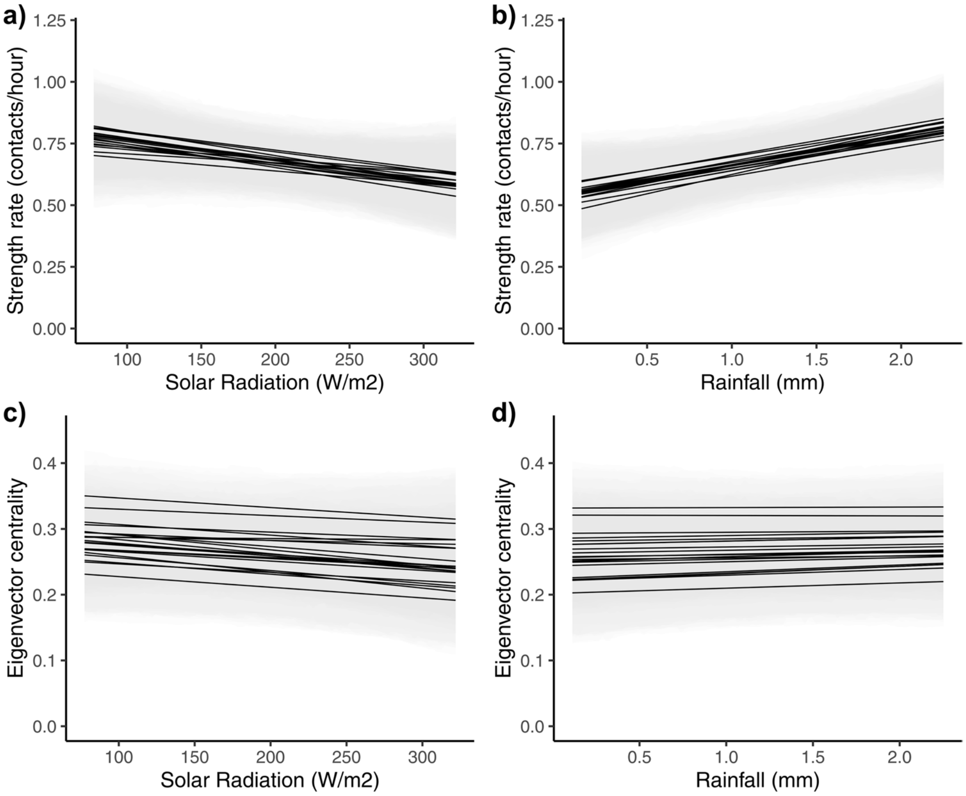

Fig. 5 Network reaction norm estimates for individual response to rainfall and solar radiation: **a**, **b** individual strength and **c**, **d** individual eigenvector centrality. Each line represents an individual estimated response, along with their 95% credible intervals as shaded grey areas

consistency of network structure suggests that these attributes are likely to be held by individuals over longer periods of time and could lead to appreciable fitness-related costs/benefits. Given that individuals were also found to alter their rate of social behaviour (i.e. grooming) in relation to both solar radiation and rainfall, it is possible that environmental conditions could speed up or slow down the spread of infections through this stable network structure. This, in turn, implies that the risk of infection for more central positions might be higher under certain environmental conditions. In our study population, where infectious disease has had drastic impacts (Barrett and Henzi 1998), and in other susceptible social species, the results of NRNs can provide insights into the propagation of infectious disease in response to environmental change.

The use of NRNs to quantify how social behaviour and structure vary in response to environmental changes facilitates various forms of comparisons across species, or within species across populations, and can provide insights into the evolution and development of social behaviour more generally (Sueur et al. 2019). For example, if we consider comparisons within species and across different study sites, it is possible to investigate whether individual variation in centrality is largely due to inter-individual differences in mean centrality (i.e. intercepts)—as our study suggests—or determine whether some populations also show greater individual differences in network plasticity and, if so, under what environmental conditions. When comparing across species, one could investigate whether phylogenetic relatedness and/or environmental conditions predict the magnitude of inter-individual differences in mean network position and/or inter-individual differences in network plasticity. Additionally, by combining NRNs of different measures, it is possible to look at both adaptability in social structuring and social behaviour, quantifying flexibility in social structure (e.g. whether and how overall network structure changes) and flexibility in social behaviour (i.e. how individuals vary their behaviour in order to compensate for environmental changes, and, potentially, act to preserve network/social structure). For example, it is generally predicted to be the case that, for primate social groups, individual behaviours will vary while social structures remain stable, whereas for other species, such as the African striped mouse (*Rhabdomys pumilio*), changes in environment can lead to drastic changes in social organisation with little change in individual behaviour (Henzi et al. 2009, 2013; Schradin 2013).

More generally, the ability to better understand and make predictions about social networks in changing environments can have direct implications for disease management, population-level dynamics, as well as other ecological and evolutionary processes where social network structures have been shown to be an influential component (Cantor et al. 2019). Additionally, increases in geospatial infrastructure have made a growing amount of environmental data available, particularly from freely available satellite remote sensing datasets (e.g. Sentinel-2, Landsat, Modis) (Turner et al. 2015; Leidner and Buchanan 2018), facilitating the integration of dynamic social networks with environmental measures. This suggests that an NRN approach could be a very useful approach for studying the response of social species to both landscape and climate changes.

Shifting towards a dynamic view of social networks will make it possible to better understand social changes in animal groups. The extension of the behavioural reaction norm framework to the analysis of dynamic social networks (i.e. NRN) offers the ability to quantify how social networks respond to environmental change and can provide necessary insights into the interaction between social and physical environments.

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Data availability The data and code used for this analysis are provided at https://github.com/tbonne/NRN.

Declarations

Competing interests The authors declare no competing interests.

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