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# Drivers and consequences of variation in individual social connectivity

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There is a growing interest in identifying specific causes and consequences of variation in individual social behaviour as a means of understanding how different individuals balance the costs and benefits of group living. In this study, we used social networks to examine variation in individual social behaviour in wild Grant's gazelles, *Nanger granti*, and explored potential drivers and consequences of this variation. First, we quantified two aspects of individual network position (weighted degree and closeness) on a monthly basis for 12 consecutive months and examined life-history (age) and abiotic (rainfall) factors that could explain among-individual variation in network position. Next, we examined the level of within-individual repeatability in network position over time. We then tested for potential consequences of this variation focusing on parasite infection and diet quality. Rainfall and age were strong predictors of variation in closeness but not degree. Interestingly, we found that one aspect of individual network position (closeness) varied over time, while another (degree) was moderately repeatable. The difference in within-individual repeatability of the two measures may be explained by the dependence of closeness on rainfall. In addition, we found that individual network position had consequences for both parasitism and diet, but the magnitude and direction of these effects depended on parasite type, connectivity measure and environmental conditions. Overall, our results suggest that environmental and host factors strongly influence variability in certain aspects of social connectivity in Grant's gazelles, and that abiotic and biotic forces, together, mediate the consequences of social network position.

Identifying the costs and benefits of group living is key to understanding the mechanisms that give rise to variation in social behaviour across species (Hofmann et al., 2014). Important and general costs that shape between-species variation in social behaviour include resource competition (Janson & Goldsmith, 1995; Wrangham, Gittleman, & Chapman, 1993) and parasite transmission (Altizer et al., 2003; Côté & Poulin, 1995; Nunn, Jordán, McCabe, Verdolin, & Fewell, 2015; Rifkin, Nunn, & Garamszegi, 2012), while reduced predation risk and access to mating partners are key benefits (Baglione, Marcos, Canestrari, & Ekman, 2002; Inman & Krebs, 1987; Noë & Bshary, 1997; Olson, Haley, Dyer, & Adami, 2015; Webster, Tarvin, Tuttle, & Pruett-Jones, 2004). In the past decade, there has been a surge of interest in understanding how the costs and benefits of social living vary at the within-species level, particularly among individuals in the same population or group who vary in their degree of social behaviour (reviewed in Pinter-Wollman et al., 2013). These studies have commonly linked individual attributes such as reproductive success (Formica et al., 2012), survival (Archie, Tung, Clark, Altmann, & Alberts, 2014), food discovery (Aplin, Farine, Morand-Ferron, & Sheldon, 2012) and parasite infection risk (Rimbach et al., 2015) to differences in social behaviour. While these results reveal the possible consequences of variability in individual social behaviour, the causes of this variability are still poorly understood. Although recent work has shown that variation in individual social behaviour predicts differences in fitness (Armitage, 2012; McDonald, 2007; Ryder, McDonald, Blake, Parker, & Loiselle, 2008; Silk, Alberts, & Altmann, 2003), fully understanding how social behaviour shapes fitness requires that both drivers and consequences of individual social variation be considered simultaneously.

Parasite infection has been the focus of many studies examining the consequences of individual variation in social behaviour (reviewed in Godfrey, 2013). For instance, a number of studies have shown that an individual's number of social contacts and position in a social network can influence its risk of acquiring parasites (Drewe, 2009; reviewed in Godfrey, 2013; Godfrey, Bull, James, & Murray, 2009; MacIntosh et al., 2012; Rimbach et al., 2015;

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VanderWaal, Atwill, Isbell, & McCowan, 2014). Importantly, recent work suggests that social contacts can both enhance and reduce the risk of parasitism depending on the context, including characteristics of the host (e.g. age; VanderWaal, Atwill, Hooper, Buckle, & McCowan, 2013; VanderWaal et al., 2016) and characteristics of the parasite (e.g. transmission mode; Fenner, Godfrey, & Michael Bull, 2011; MacIntosh et al., 2012).

Less is known about resource-related consequences of individual social behaviour. Although living in larger groups is often considered to be costly due to increased food competition (Pitcher & Parrish, 1993; Ward, Webster, & Hart, 2006) or reduced quality of food resources (Drent & Van Eerden, 1980), social behaviour can also confer resource-related benefits through increased social information (Alexander, 1974; Aplin et al., 2012; Brown, 1986; Carter, Tico, & Cowlishaw, 2016; reviewed in Galef & Giraldeau, 2001; Galef & White, 1997). For example, Aplin et al. (2012) showed that in three species of wild tits (family Paridae), which live in habitats where resources are patchy, birds with high network centrality were more likely to discover and use new food patches than were birds with low centrality. This result suggests that more connected individuals have a higher probability of receiving information about the surrounding environment from conspecifics.

In contrast to the relatively large body of work on consequences of variation in individual social behaviour, the literature on drivers is sparse (reviewed in Pinter-Wollman et al., 2013). However, some studies have begun linking abiotic factors and animal life-history traits to differences in individual social behaviour. For example, Godfrey, Sih, and Bull (2013) examined social contacts between male and female sleepy lizards, *Tiliqua rugosa*, and found that the frequency of male–female associations was lower during periods of reduced rainfall, possibly because mating decreases when there are insufficient resources for successful reproduction. In male African elephants, *Loxodonta africana*, age was linked to individual social connectivity, showing that older animals were more connected. Older males were more likely to be found with members of their own age class as well as with younger males, possibly because younger males seek out older males to gain social and ecological information (Chiyo et al., 2011). Studies such as these that examine drivers of individual social behaviour can provide important insights into how variation arises.

Building off of studies that have described either drivers or consequences of variation in individual social connectivity, we integrated behavioural, environmental, life-history and ecological data to examine both the drivers and consequences of social variation simultaneously. We also explored how individual social behaviour varies over time. To do this, we quantified individual social behaviour in wild Grant's gazelles, *Nanger granti*, using social network analysis. First, we tested whether environmental and life-history variables play a role in shaping within- and between-individual variation in social connectivity. We predicted that factors such as rainfall and age would influence levels of connectivity. In terms of rainfall, we expected that more heterogeneously distributed resources during wet periods might increase levels of connectivity as individuals track resource pulses in the habitat. In terms of age, we predicted that individual connectivity would increase with age if older animals occupy more dominant or leadership roles in groups. Next, we assessed whether individual social network position changed over time by examining the repeatability of individual connectivity across the study period. We expected that the consistency of social position over time would depend on the drivers of social behaviour. If social connectivity is influenced by rainfall or age, we expected to see temporal variation in individual connectivity that mirrored changes in environment or life history. Finally, we tested for consequences of variation in individual connectivity focusing on one potential cost (parasitism) and benefit (access to food) of social behaviour. Our aim with this last objective was to better understand if there are individual-level trade-offs associated with social connectivity. We predicted that highly connected individuals might bear a parasite cost on the one hand, but show improved diet quality on the other as a result of better access to food.

## METHODS

### Study System

We focused on a population of Grant's gazelles at the Mpala Research Center (MRC) (0°17′N, 37°53′E), Kenya. MRC is located in a semi-arid region of central Kenya with annual rainfall ranging from 439 to 639 mm per year (Goheen et al., 2013). The Grant's gazelle is an arid-adapted species with a resource defence-based mating system (Walther, Mungall, & Grau, 1983). Males compete for high-quality territories to indirectly control access to females, and breeding can occur year round although mating typically peaks during the wet season (Estes, 1967; Walther, 1972). At MRC, most rainfall occurs during two distinct periods: April–May and August–October. Female gazelles at MRC are typically found in groups of 2–20 individuals within male territories (Ezenwa, 2003), but group membership is fluid and females can move between groups (Estes, 1967; Walther, 1972).

### Behavioural Observations

In 2009 and 2011, female gazelles were captured using a handheld net gun fired from a helicopter or drive nets on the ground. Average handling time per animal was 17 min and all possible precautions were taken to minimize stress. Throughout the process, a wildlife veterinarian monitored the animals. Because no drugs were used to subdue captured females, individuals resumed normal behaviour within minutes of release. Captures were performed under the authority of the Kenya Wildlife Service. Animal protocols were approved by the Institutional Animal Care and Use Committees of the University of Montana and the University of Georgia and conformed to the ASAB/ABS Guidelines for the treatment and use of animals in behavioural research (http://www.sciencedirect.com/science/article/pii/S0003347211004805).

At capture, each individual was eartagged to facilitate individual identification. All individuals were weighed to the nearest 0.5 kg, and a single observer took physical measurements, including horn length. Horn length was measured as the distance between the base and tip of the horn on the right and left sides. Age was estimated from an equation relating horn length to tooth wear developed for a subset of nine females from the same population (Ezenwa, n.d.). Beginning in June 2011, we tracked 36 individually identifiable females aged 4 years or older (range 4–13 years) for 12 consecutive months to collect data on group membership. Study individuals accounted for an estimated 30–40% of the total female gazelle population at MRC. We used regular road transects distributed throughout the day, from 0630 to 1830 hours, to locate female groups. We defined a social group as a set of two or more individuals engaged in coordinated activity that was spatially distinct from other groups at the time of observation (Fennessy, 2004). When a group was located, group size, composition (e.g. sex and age structure) and the identity of all tagged individuals were recorded. Monthly rainfall records for the study period were obtained from the Mpala Research Center.

### Parasites

Grant's gazelles are hosts to a number of faecal–oral transmitted parasites (Ezenwa, 2003; Ezenwa, Ekernas, & Creel, 2012). We looked for three main types of parasites in gazelle faecal samples: strongyle nematodes (Nematoda: Strongylida), coccidia (Apicomplexa: Eimeriidae) and lungworms (Nematoda: Protostrongylidae). Strongyles and coccidia have direct life cycles. Eggs or oocysts are passed out in the faeces, and infective stages of the parasites accumulate on vegetation or in the soil; infection occurs through ingestion of infective larvae or oocysts (Bowman, 2009). Lungworms have an indirect life cycle, which requires gastropods as intermediate hosts for parasite development. Infection occurs when ungulate hosts accidentally ingest gastropod intermediate hosts (Bowman, 2009). To estimate the intensity of these parasite infections in study animals, we collected faecal samples from individual females at capture and routinely throughout the 12-month study period. At capture, we collected faeces directly from the rectum, and after capture we collected samples noninvasively by monitoring defecations of individually identifiable animals in the field. Faeces were typically collected within 10 min of observing a defecation event, and for each sample we recorded the animal ID, time and date. All samples were kept on ice in the field until transported back to the laboratory for processing. Parasitological analyses occurred on the same day as sample collection. To quantify gastrointestinal parasites (strongyles and coccidia), we used a modified McMaster faecal egg counting technique (Ezenwa, 2003), and to quantify lungworms, we used a beaker-modified Baermann method (Ezenwa et al., 2012; Forrester & Lankester, 1997). Parasite intensity was estimated as the number of eggs, oocysts or larvae seen per gram faeces. Although the exact relationship between faecal counts and the number of adult parasites has not been established for Grant's gazelles, egg counts can serve as a valuable noninvasive indicator of relative infection rates across both domesticated and wild ungulate hosts (Bryan & Kerr, 1989; Budischak, Hoberg, Abrams, Jolles, & Ezenwa, 2015; McKenna, 1981). Of 36 females for which we had group membership data, parasite data were collected for 31. In total, we screened 328 faecal samples for parasites, with an average of 11 (range 1–24) samples per female.

### Diet Quality

To estimate individual access to food, we assessed gazelle diet quality. We did this by using the same faecal samples that were used for quantifying parasites to estimate faecal crude protein content. Dietary crude protein was estimated using near infrared reflectance spectroscopy (NIRS) (Stuth, Jama, & Tolleson, 2003). Faecal samples were dried by placing approximately 10 g in open paper bags until completely dry. The samples were stirred daily to facilitate drying and to prevent fungal growth. All samples were processed and analysed as described by Lyons and Stuth (1992). Crude protein was predicted using faecal NIRS equations developed for the domestic goat using goat:diet faecal pairs (Leite & Stuth, 1995), and values are expressed as percentages of NIRS predicted crude protein, as described in Ezenwa (2004a).

### Social Network Position

We inferred pairwise social relationships between Grant's gazelles based on group co-membership following the ‘gambit of the group’ assumption (Whitehead & Dufault, 1999). All gazelles seen in the same social group during an observation were assumed to be associating with every other gazelle in the same group. Networks consisted of all pairwise combinations of identifiable individuals in a group (Croft, Madden, Franks, & James, 2011; Franks, Ruxton, & James, 2010).

To quantify individual network position, first, we estimated edges, or the proportion of time that individuals were seen together in a social group each month using the half-weight index of association (HWI): $E_{AB} = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$, where $x$ is the number of sampling periods in which individual A and B were observed together; $y_A$ is the number of sampling periods individual A was observed but individual B was not; $y_B$ is the number of sampling periods individual B was observed but individual A was not; and $y_{AB}$ is the number of sampling periods in which individuals A and B were seen together. The HWI corrects for bias introduced by missed sightings of focal individuals, providing a closer estimate of the real rate of association (Cairns & Schwager, 1987; Whitehead, 2008a). Next, we used the HWI association matrices to calculate weighted versions (Opsahl, Agneessens, & Skvoretz, 2010) of two network measures for each individual for every month of the study: weighted degree (hereafter referred to as degree) and closeness centrality (hereafter referred to as closeness). These two indices have been widely used to understand the role of network position in parasite transmission (reviewed in Godfrey, 2013) and we chose them because they characterize different aspects of connectivity (Fig. 1). Degree measures how many edges (i.e. direct associations) a

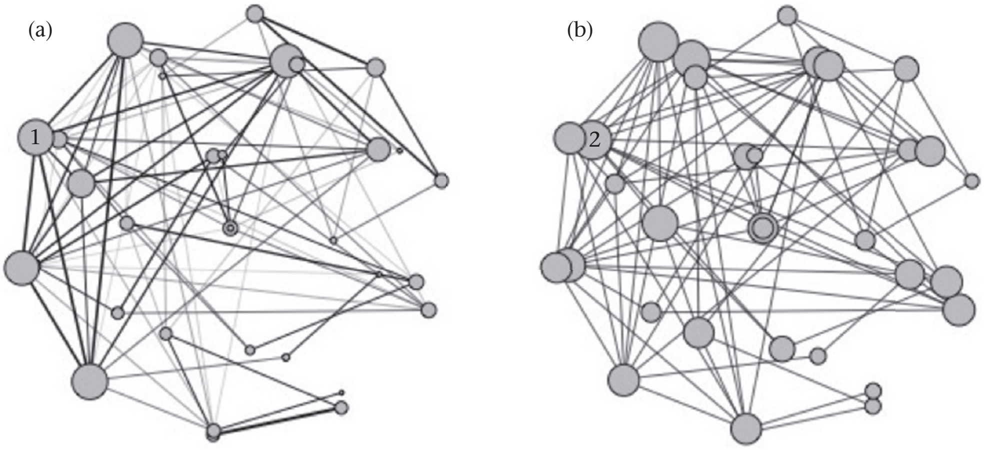

**Figure 1.** Grant's gazelle association network for a representative month (July 2011) illustrating two social connectivity measures: (a) degree and (b) closeness. Nodes (circles) represent individual gazelles ($N = 34$) and edges (lines) represent observed associations. Larger nodes represent higher (a) weighted degree and (b) closeness. Number 1 (a) indicates a node with high weighted degree and number 2 (b) indicates a node with high closeness. Edge thickness corresponds to the half-weight indices (HWIs) used to calculate weighted degree and closeness.

node (i.e. a female) has and the number of times a pair was associated (Newman, 2010). Closeness measures how well connected a node is to the rest of the network, reflecting both direct and indirect associations across the entire network (Freeman, 1978). Generally, closeness centrality is defined as the reciprocal of the sum of the shortest path lengths between the focal individual and all other individuals in the network. We used a modified version of closeness centrality defined as the sum of reciprocal shortest path lengths, where a closeness measure of 0 is assigned to unconnected nodes (Opsahl et al., 2010; Sinclair, 2009; Wasserman & Faust, 1994). We also normalized closeness for network size. All HWI calculations were performed using the R package ‘asnipe’ (Farine, 2017a), and network metrics were calculated using the R package ‘sna’ (Carter et al., 2016).

Our decision to calculate social network indices at monthly intervals was based on an evaluation of the sampling effort necessary for generating reliable social networks at multiple temporal scales. On average, 31 out of the 36 individuals were seen four or more times per month, while the remaining five individuals were seen at least three times per month. We tested the reliability of this level of sampling effort by estimating the correlation coefficient between the true and estimated indices of association as described in Whitehead (2008a, 2008b). Coefficient estimates for the monthly networks ranged from 0.76 to 0.917 (Supplementary Material, Table S1), all of which were at or above the suggested threshold for a reliable network (~0.8; Whitehead, 2008a, 2008b). Given this, we concluded that we had sufficient data at monthly intervals to reliably estimate gazelle networks on this timescale. Importantly, monthly networks provided the most biologically meaningful resolution for comparisons with the other host trait and environmental data we collected in this study. For example, rainfall, parasite and crude protein data were collected several times per month and then averaged monthly for comparison to the network metrics. The aggregation of these data at a 1-month, rather than larger (e.g. 2- or 3-month), timescale allowed us to retain as much temporal variation as possible in the data set.

### *Statistical Analyses*

To examine potential drivers of network position, we tested for associations between our two measures of network position and life-history (age) and abiotic (rainfall) predictors. We used linear mixed effects models (LMM) to account for repeated measures of individual females. We ran two models, one with degree as the response variable (Degree ~ Age + Rainfall + (1|ID)) and one with closeness as the response variable (Closeness ~ Age + Rainfall + (1|ID)), with age (in months) and rainfall (in centimetres) included as predictor variables in each model, and animal ID included as a random effect. Since rainfall was quantified as the sum of rain falling in a month, rainfall and month were correlated, so month was not included as a random effect in the models.

Next, to test for within-individual consistency in social network position, we examined the repeatability of degree and closeness over the 12-month study period. To do this, we used the rpt.remlLMM function in the rptR package in R. This function calculates repeatabilities based on within- and between-group variances estimated from LMMs. Each repeatability model was permuted 1000 times, resulting in a distribution of repeatabilities ($R_M$) from which confidence intervals were inferred (Nakagawa & Schielzeth, 2010). We tested the robustness of the repeatability scores based on monthly networks by rerunning the analyses on network metrics calculated across 3-month timescales. Repeatability estimates on both sets of networks were qualitatively similar (Supplementary Material, Table S2), so we only report the monthly results in the main text.

Finally, to examine the consequences of network position, we tested whether degree and closeness were predictors of individual parasite load and diet quality. We constructed separate models for each consequence (strongyle intensity, lungworm intensity, coccidia infection status, crude protein). Since the two network metrics were weakly correlated (Spearman rank correlation: $r_S = 0.140$, $N = 405$, $P = 0.005$) we did not include degree and closeness as predictor variables in the same models. In total, we ran eight different models, with four response variables (strongyle intensity, lungworm intensity, coccidia infection status, crude protein) and two predictors (degree, closeness).

For the parasite models, we tested the effect of network position on strongyle nematode and lungworm intensity, and coccidia infection status (i.e. presence or absence). Strongyle and lungworm data were log transformed ($\log(x+1)$) to normalize error distributions. We used linear mixed effects models (strongyles, lungworms) or a generalized linear mixed model (GLMM; binomial errors, logit link: coccidia) to account for repeated measures. Each parasite type was included as a response variable, with degree or closeness as the main predictor variable. Age, rainfall and interactions between rainfall∗network position and age∗network position were included as covariates in all models. Animal ID was included as a random effect. We constructed a similar LMM to test the effect of network position on diet quality, measured as faecal crude protein. Crude protein data were square-root transformed to normalize error distributions. For each model, we used Akaike's information criterion (AIC) and a backwards-stepwise elimination procedure to select the minimum adequate model (results from the model elimination procedure are reported in the Supplementary Material, Table S3). Model fit was evaluated by examining the distribution of residuals and plotting fitted values against residuals (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). All models were run in R (version 3.2.2) with the package lme4 (Bates, Mächler, Bolker, & Walker, 2015, version 1.1).

Since all individuals in a network are connected to some extent, individual network measures are not independent of each other. To account for this nonindependence, we calculated the significance of the network measures in our statistical models using randomization tests. Randomizations were performed on observed association data to determine whether model parameters (e.g. β estimate, $R_M$) estimated using network measures derived from the observed data differed significantly from random (Croft et al., 2011; Farine, 2017b; Farine & Whitehead, 2015). Specifically, we conducted 1000 permutations, controlling for the number and size of groups to create a set of randomized networks (Bejder, Fletcher, & Bräger, 1998; Franks et al., 2010; Manly, 1997; Whitehead, Bejder, & Ottensmeyer, 2005). Network measures were then recalculated for each randomized network and used in the same models that were used for the observed data (as described above). In all cases, *P* values were calculated by comparing model parameters obtained from the observed data to parameters obtained from the randomized data. Parameter values that fell outside 95% of the random parameter distribution were considered significant. Network permutations were conducted using the R package ‘asnipe’ (Farine, 2017a).

## RESULTS

### *Drivers of Social Network Position*

Both age and rainfall emerged as significant predictors of connectivity. Closeness was significantly and negatively associated with age (LMM: $N = 383$ observations on 34 individuals, $\beta \pm SE = -0.003 \pm 0.001$, $t = -1.706$, $P = 0.001$) and significantly and positively associated with rainfall ($\beta \pm SE = 0.017 \pm 0.005$,

$t = 3.226$, $P < 0.001$). Degree was not associated with either age or rainfall (LMM: $N = 383$ observations on 34 individuals, age: $\beta \pm SE = -0.001 \pm 0.003$, $t = -0.185$, $P = 0.244$; rainfall: $\beta \pm SE = -0.004 \pm 0.005$, $t = -0.874$, $P = 0.083$).

### *Repeatability of Individual Social Network Position*

Degree was moderately repeatable over the 12-month study period ($N = 405$ observations on 36 females, $R = 0.418$, 95% CI = (0.286, 0.539), $P < 0.001$; Fig. 2a). In contrast, closeness was not repeatable ($N = 405$ observations on 36 females, $R = 0.076$, 95% CI = (0.015, 0.153), $P = 0.154$; Fig. 2b).

### *Consequences of Social Network Position*

Degree and closeness both emerged as predictors of different aspects of parasite infection and diet quality. Degree, which reflects an individual's direct associations, was not correlated with strongyle intensity, but it was negatively correlated with lungworm intensity and positively correlated with coccidia infection status. Thus, individuals with higher degree scores had lower lungworm intensities, but they were more likely to be infected with coccidia. In contrast, degree was not correlated with dietary crude protein content (Table 1).

Closeness, which reflects how well connected an individual is across the social network, was not correlated with strongyle or lungworm intensity, but it was positively correlated with coccidia infection status. There was also a significant closeness∗rainfall interaction effect on diet quality (Table 2). Individuals with higher closeness scores had higher crude protein content in their diets during periods of low rainfall.

## DISCUSSION

Grant's gazelles have a fluid social system in which females frequently move between social groups, resulting in key differences in individual social behaviour. Our study suggests that at least some aspects of this variation in individual social connectivity are driven by environmental conditions and individual life history and have implications for parasite infection and diet quality. We quantified social connectivity using two social network metrics: weighted degree and closeness centrality. Degree, a measure of the number and strength of direct associations a female has, was linked to both parasite-related costs and benefits; whereas closeness, a measure of both direct and indirect associations, was linked to parasite-related costs and dietary benefits. Interestingly, the effects of social connectivity on parasitism depended on the type of parasite: highly connected individuals were more likely to be infected with coccidia on the one hand, but had lower lungworm burdens on the other. Similarly, the effects of closeness on diet depended on environmental context. For example, highly connected individuals had higher crude protein levels only during wet periods. Taken together, our results show that different aspects of social connectivity (in this case degree versus closeness) impose distinct costs and benefits on female gazelle. Moreover, environmental context and parasite traits appear to be critical in determining the consequences of social behaviour.

Both environment and age emerged as significant drivers of closeness in our study, suggesting that these two factors affect how well connected individual females are to the entire network. With respect to environment, individual closeness measures were higher during periods of higher rainfall. Changes in environmental conditions, such as rainfall, have been widely shown to affect social structure (Bronikowski and Altmann, 1996; Rubenstein, 1994; Wittemyer & Getz, 2007; Wrangham & Rubenstein, 1986). Moreover, previous social network studies have found that rainfall predicts temporal variation in individual network metrics. For example, in sleepy lizards, higher connectivity measures were recorded during periods of high rainfall (Godfrey et al., 2013), similar to the pattern we observed in gazelles. In lizards, it was hypothesized that increased connectivity during rainy periods was due to increased mating activity associated with better

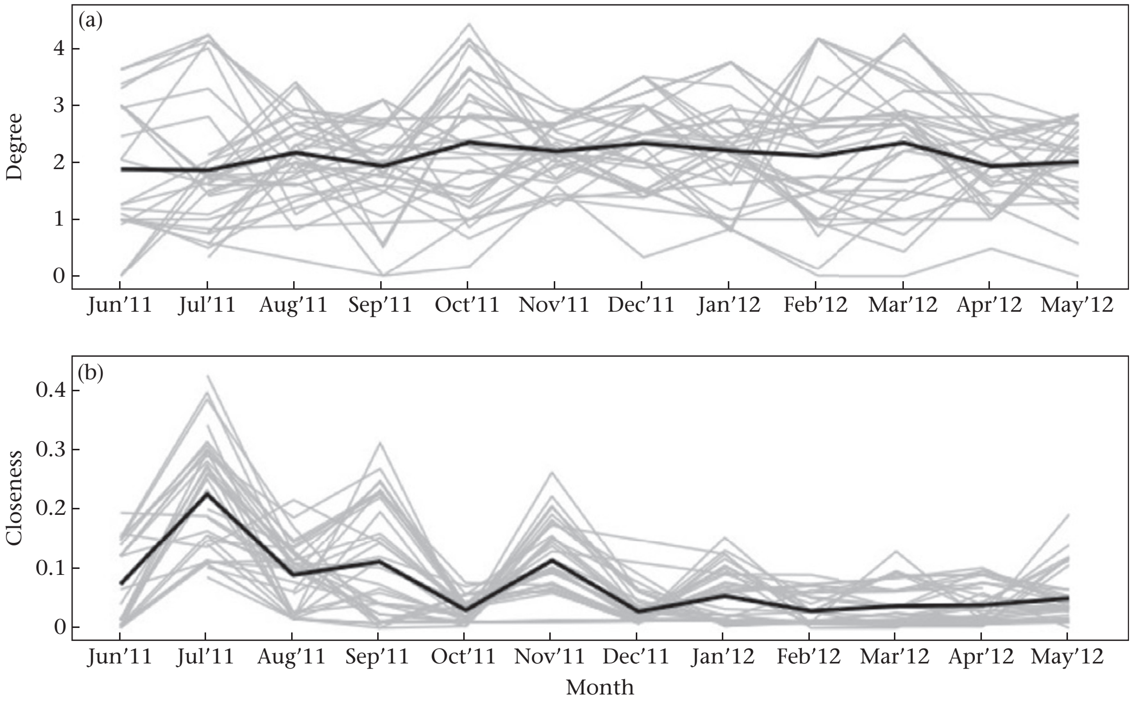

**Figure 2.** Monthly (a) degree and (b) closeness measures for 36 individuals over the 12-month study period (June 2011 – May 2012). Grey lines represent each individual; black lines show averages across all individuals.

**Table 1**
Model output showing the parasite infection and diet quality consequences of degree

| Predictor variable | Strongyle intensity (*N*=129 observations, 27 individuals) | | | Lungworm intensity (*N*=177 observations, 26 individuals) | | | Coccidia status (*N*=128 observations, 27 individuals) | | | Crude protein (*N*=167 observations, 27 individuals) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | β±SE | *t* | *P* | β±SE | *t* | *P* | β±SE | *t* | *P* | β±SE | *t* | *P* |
| Degree | −0.02±0.10 | −0.212 | 0.101 | **−0.16±0.13** | **−1.227** | **<0.001** | **0.19±0.38** | **0.496** | **<0.001** | −2.27±1.84 | −1.233 | 0.336 |
| Age | −0.001±0.01 | −0.174 | 0.222 | 0.001±0.01 | 0.080 | 0.937 | −0.27±0.30 | −0.886 | 0.376 | −0.15±0.09 | −1.703 | 0.097 |
| Rainfall | 0.02±0.01 | 1.962 | 0.053 | **0.05±0.01** | **4.073** | **<0.001** | **0.14±0.04** | **3.349** | **<0.001** | −0.17±0.47 | −0.359 | 0.720 |
| Degree∗Age | – | – | – | – | – | – | – | – | – | – | – | – |
| Degree∗Rainfall | – | – | – | – | – | – | – | – | – | 0.43±0.20 | 2.202 | 0.083 |

LMMs were used to examine strongyle and lungworm intensities and crude protein levels, and a GLMM was used to examine coccidia infection status. Basic model structure = *y* ~ Degree + Age + Rainfall + Degree∗Age + Degree∗Rainfall + (1|ID). Significant effects are shown in bold; the *P* values for degree and its interactions are based on randomization tests. The best-fit model results are shown, with dashes indicating terms from the full model that were dropped from the minimum adequate model. See Supplementary Table S3 for details on all stepwise models.

**Table 2**
Model output showing the parasite infection and diet quality consequences of closeness

| Predictor variable | Strongyle intensity (*N*=129 observations, 27 individuals) | | | Lungworm intensity (*N*=177 observations, 26 individuals) | | | Coccidia status (*N*=128 observations, 27 individuals) | | | Crude protein (*N*=167 observations, 27 individuals) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | β±SE | *t* | *P* | β±SE | *t* | *P* | β±SE | *t* | *P* | β±SE | *t* | *P* |
| Closeness | 7.81±19.08 | 0.409 | 0.529 | −47.58±30.95 | −1.537 | 0.809 | **0.21±1.21** | **0.174** | **<0.001** | −290.70±322.83 | −0.900 | 0.757 |
| Age | 0.01±0.10 | 0.115 | 0.909 | −0.18±0.19 | −0.975 | 0.336 | −0.25±0.30 | −0.847 | 0.397 | −2.84±1.54 | −1.847 | 0.069 |
| Rainfall | 0.12±0.01 | 1.717 | 0.089 | **0.05±0.01** | **4.108** | **<0.001** | **0.13±0.04** | **3.246** | **0.001** | **0.87±0.23** | **3.763** | **<0.001** |
| Closeness∗Age | −1.03±3.21 | −0.321 | 0.342 | 8.83±5.41 | 1.632 | 0.775 | – | – | – | 58.86±53.82 | 1.094 | 0.111 |
| Closeness∗Rainfall | – | – | – | – | – | – | – | – | – | **−1.70±6.22** | **−0.274** | **0.004** |

LMMs were used to examine strongyle and lungworm intensities and crude protein levels, and a GLMM was used to examine coccidia infection status. Basic model structure = *y* ~ Closeness + Age + Rainfall + Closeness∗Age + Closeness∗Rainfall + (1|ID). Significant effects are shown in bold; the *P* values for closeness and its interactions are based on randomization tests. The best-fit model results are shown, with dashes indicating terms from the full model that were dropped from the minimum adequate model. See Supplementary Table S3 for details on all stepwise models.

environmental conditions. In Grant's gazelles, mating occurs year round with peaks during the rainy season (Estes, 1967), but it is unlikely that mating alone explains the rainfall–connectivity pattern in this species. Grant's gazelles have a resource defence polygyny-based mating system where females track resources and males actively defend patches of resources (i.e. territories) that are attractive to females in order to enhance their mating opportunities (Estes, 1974; Jarman, 1974; Walther et al., 1983). However, male territories can vary greatly in the quality of food resources they contain (Augustine & McNaughton, 2004), both in space and in time; the latter as a result of the often patchy distribution of rainfall in our study area (Franz, Caylor, Nordbotten, Rodríguez-Iturbe, & Celia, 2010). Thus gazelle territorial structure, patchy rainfall and resource tracking may explain why rainfall is a predictor of closeness. In particular, females from different social groups may cluster on the same high-quality territories during periods of high rainfall as a result of resource tracking. This behaviour should increase connectivity across the entire network, elevating closeness.

In terms of life history, age was negatively associated with closeness, with younger individuals having higher measures of closeness than older individuals. Social association patterns and network position have previously been shown to vary with age (Chiyo et al., 2014; Hirsch, Stanton, & Maldonado, 2012; Patriquin, Leonard, Broders, & Garroway, 2010). For example, age was associated with initiating and receiving affiliative interactions (e.g. greeting, allogrooming, play behaviour) in yellow-bellied marmots, *Marmota flaviventris*. In these affiliative networks, younger marmots had higher in-closeness measures, receiving more affiliation from direct and indirect connections than did older individuals (Wey & Blumstein, 2010). In our study, the youngest individuals were young adults (4 years old) and not juveniles, who tend to strictly associate with their mothers (Walther, 1972). Thus, our data suggest that younger adult female gazelle are more likely to move between groups, possibly because they are actively establishing social relationships. Such behaviour has been reported in female horses, *Equus caballus*, for example, where younger individuals interact with different social groups for a few years before choosing a more permanent group (Linklater & Cameron, 2009). It is also possible that younger adult female gazelles are forced out of social groups by older females, as occurs in ringtailed coatis, *Nasua nasua* (Hirsch, 2011). This type of age-related aggression could also produce the age–closeness pattern that we observed.

Intriguingly, the repeatability of our two measures of individual connectivity over time reflected the amount of influence environment and life history had on each measure. Closeness, which was predicted by rainfall and age, was not repeatable. Individual females showed no consistency in closeness over time. Since rainfall is also a driver of temporal variation in food availability at our study site (Augustine & McNaughton, 2004), it is likely that rainfall-driven changes in resource distributions influence female behaviour in ways that account for within-individual flexibility in closeness measures. In support of this idea, work on other species has also linked resource availability to changes in social connectivity. For example, killer whales, *Orcinus orca*, have less connected social networks in times of low salmon abundance (which make up the largest proportion of their diet) compared to times of high salmon abundance, possibly because individuals spread out to search for other prey when salmon are scarce and spend less time being social (Foster et al., 2012).

In direct contrast to closeness, degree scores in gazelles were fairly consistent within an individual over time. Work on wild great tits, *Parus major* (Aplin et al., 2015), and captive small spotted catsharks, *Scyliorhinus canicula* (Jacoby, Fear, Sims, & Croft, 2014), has also shown repeatability in degree over time. Since the weighted degree index that we used accounts for both the number of associates a female had and the number of times a particular association occurred, the moderate repeatability of this network position may indicate individual preferences for particular group sizes. For example, in great tits, repeatable weighted degree measures corresponded with consistent individual group size choice (Aplin et al., 2015). Moreover, in spotted catsharks, individual preference for group size was a strong driver of repeatable levels of weighted degree, even across different habitat types (Jacoby et al., 2014). In our study population, degree was positively correlated with group size (Spearman correlation: $r_S = 0.386$, $N = 405$ observations, $P < 0.001$), so it is possible that this measure, unlike closeness, is shaped by social forces (e.g. the manifestation of individual group size preferences) rather than environmental forces, explaining both the higher level of within-individual consistency over time in this measure as well as its lack of association with environmental and life-history drivers. Future work is needed to fully explore the potential role of individual social preferences in shaping degree in gazelles.

Several key consequences of social connectivity also emerged in our study. Network position influenced parasite infection status and diet, but these consequences were mediated by other factors including the type of parasite, the specific measure of social connectivity considered and the environment. First, the distinct relationships we observed between degree and closeness and different types of parasites suggest that the consequences of individual connectivity for parasite transmission depend on the biology of the parasite in question. For example, we found that degree and closeness had no effect on strongyle nematode burden, but were positively associated with coccidia infection status. These different patterns may reflect the fact that parasites vary considerably in the breadth of hosts, which they can infect, with key implications for transmission. For instance, coccidian parasites of ungulates are known to be relatively host specific and transmission between host species is rare (Ezenwa, 2003; Levine & Ivens, 1986); whereas most strongyle nematodes are generalist parasites (Matthee, Krecek, & McGeoch, 2004; Zaffaroni et al., 2000) that infect multiple host species, allowing for extensive between-species transmission (Archie & Ezenwa, 2011). These differences suggest that coccidia transmission in gazelles may be more dependent on intraspecific interactions than is strongyle transmission, resulting in the positive association between host social network metrics and coccidia status and the lack of association between network metrics and strongyle intensity. This idea is supported by our past work showing that for both Grant's gazelles and other sympatric ungulates, such as impala, *Aepyceros melampus*, at our study site, strongyle burdens are better predicted by interspecific rather than intraspecific contact, whereas coccidia burdens are better predicted by intraspecific than interspecific contact (Ezenwa, 2003, 2004b).

Variation in lungworm burden was explained by only one of our social connectivity measures: degree. Other studies have also reported distinct relationships between different measures of individual connectivity and parasite infection risk, suggesting that variation in the extent to which different aspects of connectivity predict parasite consequences is relatively common. For example, female Japanese macaques, *Macaca fuscata yakui*, with higher eigenvector centrality, a measure of influence, in an outward grooming network (i.e. grooming given) were more likely to be infected by the gastrointestinal nematode *Strongyloides fuelleborni*. However, weighted degree in the same grooming network was not associated with infection status (MacIntosh et al., 2012). Likewise, a more recent study on brown spider monkeys, *Ateles hybridus*, focused on weighted degree, closeness centrality and betweenness centrality (a measure of the extent to which an individual acts as a 'bridge' in a network; Freeman, 1978), found that degree and betweenness, but not closeness, were positively associated with *Strongyloides* infection (Rimbach et al., 2015).

Counterintuitively, the relationship between degree and lungworm intensity in gazelles was negative. Individuals with high degree scores had lower lungworm burdens than those with low degree scores. Explaining this negative relationship is challenging because the biology of the lungworms that infect gazelles is not well known, yet general aspects of lungworm biology may prove relevant in explaining the pattern. Typically, lungworms in ungulates are transmitted by a gastropod intermediate host, so it is possible that the negative relationship between degree and lungworm burden reflects a type of 'dilution effect', a phenomenon often seen for mobile parasites, where the probability of an individual being attacked by a mobile parasite decreases with increasing group size (Côté & Poulin, 1995; Mooring & Hart, 1992; Rubenstein & Hohmann, 1989). Gazelles with higher degree might ingest fewer infected gastropods if feeding in larger aggregations dilutes the risk of accidentally ingesting a gastropod as these organisms are depleted by conspecifics. Interestingly, this potential effect of the local pool of conspecifics on an individual's probability of ingesting an infected gastropod may help explain why degree (which quantifies direct associations) is a better predictor of lungworm intensity than is closeness (which accounts for both direct and indirect associations). More generally, no other studies, to our knowledge, have described a negative relationship between individual social connectivity and nematode intensity. This may be because most studies on this topic focus on directly transmitted rather than indirectly transmitted parasites. As new data accumulate it will be interesting to explore whether patterns of association between social network position and levels of parasitism differ predictably with respect to certain parasite traits as has been demonstrated for associations between group size and parasitism (Côté & Poulin, 1995).

As with parasitism, the effects of network position on diet quality depended on the specific aspect of social connectivity being considered and on other factors, in this case environmental conditions. First, associations between social network position and diet only emerged for closeness and not degree. Since closeness reflects the distance between an individual and all others in the network, it may better capture the social information individuals receive about food resources (Croft, James, & Krause, 2008). Thus, high closeness may increase the chance that a gazelle learns about resource hotspots improving its access to food (Aplin et al., 2012). Second, individuals with higher closeness scores had higher crude protein levels only during dry periods, gaining no benefit during wetter periods. This may reflect an information flow benefit for more connected gazelles during poor conditions when high-quality food is hard to find. In contrast, information derived from conspecifics may have less of an impact on diet quality during wet periods if individuals have similar access to information about food (e.g. via environmental-based cues). Finally, it is important note that degree may not have emerged as a positive predictor of food quality in our study because of resource competition. When defining associations using group membership, weighted degree is roughly proportional to the average group size (Jarman, 1982). Indeed, degree and group size were positively correlated in our data set (see above). A major cost of group living is an increase in food competition, especially when food patch quality varies (Hirsch, 2007), resulting in reduced individual food intake (Janson, 1988). Thus, competition with conspecifics for resources, particularly during the dry season, may negate any social information benefits of high degree.

Overall, the factors that shape variation in individual social connectivity and the costs and benefits of this variation are key to understanding individual fitness (Formica et al., 2012; McDonald, 2007; Silk et al., 2003; Wey & Blumstein, 2012) and the evolution of social behaviour (Hofmann et al., 2014; Silk, 2007). Studies on drivers and consequences of social connectivity have uncovered a number of important insights, but few studies have investigated both simultaneously. Here, we integrated behavioural, environmental, life-history and ecological data to examine the drivers of individual social network position, how network position varies over time and the consequences of this variation. Our results indicate that environmental conditions and host traits can drive variation in social connectivity, and that the costs and benefits of connectivity are mediated by both environmental conditions and parasite traits. Importantly, we found that examining different aspects of social connectivity helped reveal more nuanced relationships.

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## Supplementary material

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