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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