



The influence of demographic variation on social network stability in wild vervet monkeys



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From a cognitive point of view, management and knowledge of social relationships is thought to be very challenging. Because of ecological and demographic constraints, relationships are likely to be prone to variation and hence need constant updating. Social network analysis is a potential tool to quantify the information that needs to be processed. However, despite the growing number of studies on social networks, few have focused on their dynamics and how they evolve across time. Here we present one of the rare studies that tests the influence of demographic variation on social relationships' stability through temporal analysis. Using field data collected on three wild groups of vervet monkeys, *Chlorocebus aethiops*, we first analysed the relationships' stability by running correlations between 3-month periods. Then, we investigated how natural demographic variation changed individual centralities (eigenvector) and strength of dyadic relationships within both grooming and proximity networks over a period of 2 years. In vervets, females are philopatric, while males emigrate from their natal group. Thus, we tested whether changes in demography had more influence on network centrality measures and relationship strength in females and their juveniles than in males. Correlations between periods yielded no evidence that predictability of future relationship quality declined with time from current relationship quality. In addition, male immigration was mostly responsible for increases in the core group members' centrality while male emigration had the opposite effect. Regarding dyadic relationships, we found inconsistent patterns that varied with respect to how age/sex and immigration/disappearance affected the network studied (grooming versus proximity). Our findings support the idea that social networks are dynamic structures that vary through time. Similar analyses on other species are needed to investigate which network features emerge as candidates responsible for variation in the complexity with which individuals keep track of relationships.

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Group living provides many advantages such as decreased predation risk and increased competitiveness against other groups of conspecifics for resources (Alexander, 1974; Wrangham, 1980; Van Schaik, 1983). However, group-living individuals face various challenges such as competition with other group members over resources and reproductive opportunities (Clutton-Brock et al., 2006). Consequently, individuals are under selection to find the right balance between cooperation and competition with the other

group members, which are also flexible in their decisions and social strategies. Previous studies strongly suggest that successful management of social relationships increases an individual's fitness. For example, early socioecological models proposed that, in situations with a high degree of within-group contest competition over food, females should evolve highly differentiated social relationships consisting largely of coalitions with kin that increase the ability to monopolize food resources, resulting in a linear and matrilineal dominance hierarchy (e.g. Isbell & Young, 2002; Sterck, Watts, & van Schaik, 1997) with the most central females having a higher fitness. Predation influences the emergence of different strategies to increase individual fitness inside the group, which in turn affects the emergence of predictable spatial associations (Byrne, Whiten, & Henzi, 1990; Heathcote, Darden, Franks, Ramnarine, & Croft, 2017;

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Janson & Goldsmith, 1995). Group members in the centre of the group have a lower probability of suffering predator attacks than individuals at the periphery (Hamilton, 1971; King et al., 2012). Information sharing within the group is another process that might lead to variation in fitness according to social relationships. Information sharing might be useful for group members not only to find resources (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), but also to learn key knowledge for survival and behavioural traditions, such as which foods are good to eat for juveniles, tool use, self-medication or predator recognition (Griffin, 2004; Huffman, 1997; Nagell, Olguin, & Tomasello, 1993). Social learning about food resources is well established in primates, but this mechanism also exists in other taxa including insects (Battesti et al., 2015; Leadbeater & Chittka, 2007). Strong social relationships favour the diffusion of information (Claidière, Messer, Hoppitt, & Whiten, 2013). In this way, individuals with multiple strong social relationships are important for information sharing (Duboscq, Romano, MacIntosh, & Sueur, 2016; Sueur, Deneubourg, & Petit, 2012; Watson et al., 2017). In female baboons, maintaining strong and stable social bonds correlates with increased offspring survival (Silk, Alberts, & Altmann, 2003; Silk et al., 2009) and longevity (Silk et al., 2010a). Another study documented that female baboons form stable social relationships with preferred partners whereas relationships with less preferred partners are more prone to variation (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012), suggesting that individuals make strategic decisions about relationship management. More interestingly, adjustments of social relationships also occur over a short timescale (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009; Sick, Marshall, Knapp, Dabelsteen, & Cowlshaw, 2014). Such studies show how important it is to study different types of relationships, their quality (e.g. Duboscq, Romano, Sueur, & MacIntosh 2016) and especially their development and variation through time (Boucherie, Sosa, Pasquaretta, & Dufour, 2016; Ilany, Booms, & Holekamp, 2015; Ilany, Barocas, Koren, Kam, & Geffen, 2013).

Changes in social relationships might be partly due to environmental variation (Henzi et al., 2009; Ilany et al., 2015; Sick et al., 2014). For example, high predictability, biomass and density of prey in the Iceland population of killer whales, *Orcinus orca*, strongly influence the social association patterns which, unlike those of other populations, lack a clear hierarchy (Tavares, Samarra, & Müller, 2017). However, it is also highly likely that natural demographic variation plays an important role (Barrett, Henzi, & Lusseau, 2012). In many species, at least some group members migrate to prevent inbreeding (see Moore, 1993 for review) while new generations of infants are regularly integrated and old individuals disappear. Consequently, group composition is subject to change and relationships are modified, not only at the dyadic but also at the group level. Trying to understand how demographic variation impacts the social structure within a group might help us describe how individuals manage their relationships.

Successful management of relationships might also be the precursor for the evolution of advanced cognitive processes and, correspondingly, brain size in social species (Pasquaretta et al., 2014; Whiten & Byrne, 1997; de Waal, 1982). It has been argued that group-living individuals have to keep track of their own social relationships as well those of other group members to compete successfully within their group (Harcourt, 1988). Usually such information is obtained through eavesdropping on social interactions within a communication network (McGregor, 2005). It has been shown that such third-party relationship knowledge is widespread throughout various taxa (primates: Bachmann & Kummer, 1980; Bergman, Beehner, Cheney, & Seyfarth, 2003; Borgeaud, van de Waal, & Bshary, 2013; Cheney & Seyfarth, 1990; Cheney, Seyfarth, & Silk, 1995; Crockford, Wittig, Seyfarth, & Cheney, 2007; Schino,

Tiddi, & Di Sorrentino, 2006; Silk, 1999; Slocombe & Zuberbühler, 2007; hyaenas: Engh, Siebert, Greenberg, & Holekamp, 2005; rats: Davis, 1992; fish: Bshary, 2002; Grosenick, Clement, & Fernald, 2007; birds: Paz-y-Mino, Bond, Kamil, & Balda, 2004). There is also some largely anecdotal evidence that primates use this knowledge in strategic behaviours such as coalition formation, manipulation or tactical deception (Cheney & Seyfarth, 1990; Kummer, 1967; Slocombe & Zuberbühler, 2007; Whiten & Byrne, 1997). However, as group size increases, these strategic behaviours are likely to be increasingly cognitively demanding as the number of dyads an individual must monitor increases exponentially (Dunbar, 1992; Lehmann, Korstjens, & Dunbar, 2007; Sueur, Deneubourg, Petit, & Couzin, 2011).

Assessing an individual's relationship quantity and quality is a first step towards understanding its relationship management. The use of social network analyses has greatly helped in this endeavour and such analyses have been employed in many studies of various taxa (Croft, James, & Krause, 2008; Krause, Croft, & James, 2007; Whitehead, 2008), including nonhuman primates (Flack, Girvan, de Waal, & Krakauer, 2006; Henzi et al., 2009; Sueur & Petit, 2008; Sueur, Jacobs, Amblard, Petit, & King, 2011). Network analyses investigate the position that an individual occupies within its group and therefore the importance of its social role, for example within a hierarchy or within a grooming network (Brent, Lehmann, & Ramos-Fernandez, 2011; Sueur, Petit et al., 2011). Centrality measure is a way to quantify an individual's importance in a group according to its position in the network. Previous studies found that individuals from the philopatric sex, which generally remain in their natal group throughout their lives, are more central within a network as they are more likely to form strong and long-lasting bonds with other group members, especially their kin (Lehmann & Ross, 2011; Matsuda et al., 2012; Smuts, 1985; Sosa, 2016). Furthermore, previous studies found that high-ranking individuals occupy a more central position within a grooming network as they receive more grooming (Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2011; Sade, 1972; Sueur, Petit et al., 2011; Watts, 2000; see Schino, 2001 for a meta-analysis). A potential explanation for such asymmetric grooming patterns is that grooming can be exchanged for tolerance around food resources and/or coalitional support (Seyfarth, 1977).

So far, social network analyses have been used to test for the emergence, development and evolution of complex social systems. However, these studies examined static social networks. In reality, relationships between individuals are dynamic and can fluctuate over time according to external ecological, social and other conditions. Only a few studies have integrated such dynamics in their analyses (Blonder & Dornhaus, 2011; Croft et al., 2008; reviewed in Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Pinter-Wollman et al., 2013). These include investigations of how dyadic association patterns are modified according to seasonal or resource variation (chacma baboons, *Papio hamadryas ursinus*: Henzi et al., 2009; Asian elephants, *Elephas maximus*: de Silva, Ranjeewa, & Kryazhimskiy, 2011; spotted hyaenas, *Crocuta crocuta*: Holekamp, Smith, Strelieff, Van Horn, & Watts, 2012; Ilany et al., 2015), how simulated and natural individual knock-outs influence the whole social network (Barrett et al., 2012; Kanngiesser et al., 2011) or the temporal stability of dyadic relationships (bottlenose dolphins, *Tursiops truncatus*: Connor, Heithaus, & Barre, 2001; spider monkeys, *Ateles geoffroyi*: Ramos-Fernandez, Boyer, Aureli, & Vick, 2009; monk parakeets, *Myiopsitta monachus*: Hobson, Avery, & Wright, 2013; primates: Dufour, Sueur, Whiten, & Buchanan-Smith, 2011). However, few studies have focused on how modifications in group composition influence the whole social network and consequently its degree of stability (Barrett et al., 2012; Borgeaud, Sosa, Sueur, Bshary, & van de Waal, 2016; Boucherie et al., 2016; Kanngiesser et al., 2011).

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