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Consistent individual variation across interaction networks indicates social personalities in lemurs

Ipek G. Kulahci [a, b, *], Asif A. Ghazanfar [a, c, d], Daniel I. Rubenstein [a]

[a] Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, USA
[b] Biological, Earth and Environmental Sciences, University College Cork, Ireland
[c] Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA
[d] Department of Psychology, Princeton University, Princeton, NJ, USA

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Group members interact with each other during multiple social behaviours that range from aggressive to affiliative interactions. It is not known, however, whether an individual's suite of social behaviours consistently covaries through time and across different types of social interactions. Consistent social behaviour would be advantageous in groups, especially when individuals need to remember their group members' social roles and preferences in order to keep track of social relationships and predict conspecifics' future behaviour. Here, we address whether social behaviour of ringtailed lemurs, *Lemur catta*, is consistent through time and across four interaction networks (aggression, grooming, contact calling, scent marking). We quantified variation in social behaviour through four network centrality measures including outdegree, outstrength, betweenness and eigenvector centrality. Comparing lemurs' measures across 2 years revealed that network centrality remained consistent between years. Lemurs' centrality also stayed consistent across interaction networks: individuals with high centrality in one interaction network also had high centrality in the other networks, even when we controlled for sex-based variation in social behaviour. Thus, regardless of their sex, some individuals were highly social and frequently groomed others, initiated aggressive interactions and responded to others' contact calls and scent marks. Lemurs also had preferred social partners they frequently interacted with across years and across multiple behaviours. In particular, lemurs frequently responded to the contact calls and the scent marks of the conspecifics they had frequently groomed. Together, these results demonstrate that individual variation in lemur social behaviour is not context specific, but instead persists through time and across multiple social interactions. Such consistent behaviour provides evidence of social personalities, which may influence individuals' interaction styles, including how socially active they are and with whom they interact.

Individual variation in social behaviour has key consequences for resource access, mate choice, disease transmission, learning, decision making and fitness (Cameron, Setsaas, & Linklater, 2009; Croft et al., 2009; Frère et al., 2010; Krause, Croft, & James, 2007; Lusseau & Conradt, 2009; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Seyfarth, Silk, & Cheney, 2012; Weidt, Hofmann, & König, 2008; Wey, Blumstein, Shen, & Jordán, 2008). Some of this variation can be attributed to age, sex, dominance and environmental factors (Monclus, Cook, & Blumstein, 2012; Seyfarth, Silk, & Cheney, 2014; Silk, Altmann, & Alberts, 2006, Silk, Alberts,& Altmann, 2006; Taborsky & Oliveira, 2012). However, variation in social behaviour may also result from some individuals being more social and initiating more interactions than others regardless of their age, sex or dominance status. Such variation may even persist through time and across different types of social interactions. For instance, socially active individuals may frequently groom others while also frequently initiating aggressive interactions.

Social differences that persist through time and across behaviours may provide insight into social personality traits. Human social personalities are identified through consistencies in social activity levels and interaction styles. Social personalities are inferred from measures such as how many interaction partners an individual has, how frequently they interact with others and the identities of their preferred interaction partners (Clifton, 2013; Fang et al., 2015; Golbeck, Robles, Edmondson, & Turner, 2011; John & Srivastava, 1999; Quercia, Lambiotte, Stillwell, Kosinski, &

* Correspondence: I. G. Kulahci, Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.
E-mail address: ipek.kulahci@gmail.com (I. G. Kulahci).

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Crowcroft, 2012; Staiano et al., 2012). Thus, social personalities can be expressed two ways. Individuals may display consistent social activity levels and they may also have preferred partners with whom they consistently interact during multiple behaviours. Given the high diversity of animal interactions, we propose that an empirical approach similar to that of human social personalities can be utilized to study animal social personalities.

Animal social personalities would have major consequences for how individuals navigate through social environments that feature repeated interactions. Over the past decade, great progress has been made in understanding animal personalities (also referred to as 'behavioural syndromes' or 'temperament') from intraindividual consistencies in exploration, boldness and activity levels (Bell, 2007; Biro & Stamps, 2008; David, Auclair, & Cézilly, 2011; Dingemanse & Réale, 2005; Koolhaas et al., 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007, Réale, Dingemanse, Kazem, & Wright, 2010; Seyfarth et al., 2012; Sih, Bell, & Johnson, 2004; Smith & Blumstein, 2008; Wolf & Weissing, 2012). On one hand, consistent behaviour frequently results in trade-offs and may reduce an individual's ability to quickly respond to changing conditions (Sih et al., 2004, Sih, Bell, Johnson, & Ziemba, 2004). On the other hand, consistent social behaviour may be advantageous in groups, especially when individuals need to remember each other's social roles and preferences. Doing so would allow them to predict the future behaviour of others and to modify their own social responses (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Reducing uncertainties during social interactions is highly advantageous (Barrett, Henzi, & Lusseau, 2012), and keeping track of others' social personalities may allow animals to reduce uncertainties about their social environment. Furthermore, as individuals vary in their sociability (i.e. response to presence or absence of a conspecific) and aggressiveness (i.e. agonistic interactions towards others) (Réale & Dingemanse, 2010; Réale et al., 2007), consistent variation in these traits may create social niches that reflect individuals' roles in the social environment (Bergmuller & Taborsky, 2010; Montiglio, Ferrari, & Réale, 2013). Social niches can be beneficial at the population level by increasing behavioural diversity, which is essential for dealing with environmental changes (Caro & Sherman, 2011; Rubenstein, 2016).

Identifying social personalities requires analysing individual variation in social behaviour through time and across behaviours. Social network analysis is a robust tool for quantifying social centrality by determining the extent of individuals' connections (Lusseau & Newman, 2004; Wassermann & Faust, 1994). Network position and centrality have multiple consequences (reviewed in Krause, James, Franks, & Croft, 2014). Network position can influence information acquisition (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Kulahci et al., 2016), disease transmission (Duboscq, Romano, Sueur, & MacIntosh, 2016; Godfrey, Bull, James, & Murray, 2009; Rubenstein, 2015) and reproductive fitness (McDonald, 2007). Social centrality can be defined in multiple ways depending on the question of interest. For instance, some centrality measures address the number of connections an individual has, some measures utilize the frequency of connections, while other measures account for the social importance of one's connections to determine their social centrality (Lusseau & Newman, 2004; Wassermann & Faust, 1994). Using multiple centrality measures is advantageous for analysing different aspects of variation in social behaviour. Similar to inferring personality traits such as boldness, exploration or neophobia from consistencies in behavioural measures through time and across contexts, we can infer social personality traits from consistencies in network centrality measures through time and across contexts (Krause, James, & Croft, 2010; Wilson, Krause, Dingemanse, & Krause, 2013). Social individuals with high centrality in one behaviour, such as aggression, may have high centrality in other behaviours such as grooming.

Several studies have utilized association networks based on physical proximity to address whether network position stays consistent through time (Aplin et al., 2015; Jacoby, Fear, Sims, & Croft, 2014; Krause et al., 2016; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015). Additional studies have addressed individual consistencies in aggressive interactions (Frumkin et al., 2016), including potential consistencies between social and defensive aggression (Blumstein, Petelle, & Wey, 2013). Yet, only a few studies have explored consistencies across networks based on different types of social behaviours (Castles et al., 2014; Madden, Drewe, Pearce, & Clutton-Brock, 2011). Thus, whether or not individual's network centrality and choice of interaction partners remain stable both through time and across different types of social behaviours has not yet been established.

We studied ringtailed lemurs, *Lemur catta*, to detect individual consistencies through time and across different social behaviours. We constructed networks from four behaviours including (1) grooming, (2) aggressive interactions, (3) contact calling and (4) scent marking. Each of these behaviours has a different function. Affiliative interactions such as grooming are essential for forming social bonds, hygiene maintenance, reducing aggression and reducing stress (Barton, 1985; Cords, 1997, pp. 24–49; Enquist & Leimar, 1993; Silk, 2007; Silk & Altmann, 2006). Strongly bonded lemurs frequently groom each other to maintain their social bonds (Kulahci, Rubenstein, & Ghazanfar, 2015). In comparison to grooming, aggressive interactions are important in intra and intersexual competition, territoriality, group stability and dominance in many species including ringtailed lemurs (Clutton-Brock et al., 2006; Flack, Girvan, de Waal, & Krakauer, 2006; Marler, 1976).

While grooming and aggression are direct interactions that involve physical contact, animals also interact indirectly through social signals. Social signals allow conspecifics to communicate when they are separated from each other and are thus comparable to an interaction. Signals can influence association and interaction networks, and they play a critical role in individual recognition, which is necessary for selectivity in social interactions (Kulahci & Ghazanfar, 2013, pp. 3–27; Kulahci, Drea, Rubenstein, & Ghazanfar, 2014; Snijders & Naguib, 2017). For instance, in many primate species including lemurs, contact calls carry individual signatures and allow group members to keep in touch over long distances (Macedonia, 1993). Besides contact calls, scent marks carry individual signatures, and investigating a scent mark provides information on the scent owner's identity, reproductive status and location (Charpentier, Boulet, & Drea, 2008; Kappeler, 1998; Scordato & Drea, 2007). In lemurs, scent marking is critical in communication, reproductive status advertisement and territoriality (Kappeler, 1998; Kulahci et al., 2014; Macedonia, 1986, 1993; Scordato & Drea, 2007). We focused on these four social behaviours to determine whether individual variation in social activity levels and interaction partners persisted through time and across behaviours with different functional consequences.

We predicted that social variation that persisted through time and across different types of behaviours would indicate presence of social personalities in lemurs. We utilized two complementary approaches to infer social personalities. First, we analysed consistencies in centrality metrics to explore whether individuals had consistently high (or low) centrality through time and across the four behaviours. We predicted that some lemurs would be more social and thus have higher network centrality than others, and that this variation would be carried over through time and across different types of behaviours, resulting in consistencies in network

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