



Understanding repeatability and plasticity in multiple dimensions of the sociability of wild female kangaroos



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Sociability, how individuals interact with conspecifics, is considered to be a key axis of animal personality. Consistent differences between individuals in measures of sociability have been demonstrated in some taxa, yet individuals also exhibit plasticity in their sociability across differing ecological conditions, particularly in gregarious species that do not occur in stable cohesive groups. Although repeatability and plasticity of measures of sociability are both important for understanding animal personality they have rarely been studied concurrently. Between and even within species, multiple behaviours have been considered to represent sociability, but there is still little understanding of the degree to which different measures of sociability reflect distinct traits. In this study, our first aim was to determine the repeatability of four different measures, representing two broad aspects of individual females' sociability, in a wild population of eastern grey kangaroos, *Macropus giganteus*. Our second aim was to investigate how shorter-term environmental conditions and individuals' states related to plasticity in these measures. Using data collected each month over a 5-year period on over 100 adult females, we analysed factors contributing to variation in individuals' grouping patterns (to reflect general gregariousness) and in the number of different conspecifics with which individuals associated (their 'choosiness' of social partners). Rainfall, body condition and reproductive state were all related to females' mean group sizes, and females with older dependent young foraged further from their neighbours. Females were more selective about group members when there was more food, and when they were in poor or excellent body condition. Although social preferences exist among females in this population, and females' measures of sociability are repeatable and differ between individuals over the long term, these current findings suggest that the influences of individuals' states and environmental conditions contribute to variation in females' patterns of sociability over shorter periods.

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Individuals within a species or population often differ consistently in how they respond to and interact with conspecifics (their sociability; Kohn, King, Dohme, Meredith, & West, 2013). The adaptive value of sociability has received increasing attention in recent years (Silk, 2007). Individual differences in sociability can relate to outcomes linked to fitness, such as natal dispersal patterns (Blumstein, Wey, & Tang, 2009; Cote & Clobert, 2007), reproductive success (Cameron, Setsaas, & Linklater, 2009; Silk, Alberts, & Altmann, 2003; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015), and survival and longevity (Silk et al., 2010; Stanton

& Mann, 2012; Weiss, Gartner, Gold, & Stoinski, 2013). However, although sociability has been considered as one of the five key axes of animal personality (Réale, Reader, Sol, McDougall, & Dingemanse, 2007) and relates to fitness, the factors that drive and maintain differences between and plasticity within individuals in sociability have not been as well studied as has been the case for some other aspects of animal personality (Aplin et al., 2015).

Despite the findings that being more sociable can confer reproductive and fitness advantages in group-living mammals, highly sociable individuals can also suffer costs to fitness (e.g. Johnson, 1986; Wey & Blumstein, 2012), potentially relating to resource competition and population density. The costs and benefits of being sociable are likely to depend on ecological context, and indeed spatial and temporal environmental variation are thought to contribute to the evolution and maintenance of

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consistent individual differences in personality traits (Wolf & Weissing, 2010). Despite the repeatability of personality traits, they nevertheless show some plasticity and the degree of plasticity in such measures can also vary between individuals (Carter, Goldizen, & Heinsohn, 2012; Dingemanse & Wolf, 2013), suggesting that plasticity itself may be a personality trait. A full understanding of the fitness consequences and evolution of personality traits requires an understanding of both the levels of repeatability (within-individual consistency) of traits and the causes and levels of plasticity in those traits. Few studies have yet investigated either of these across multiple dimensions of sociability, particularly those involving relationships among individuals.

Since multiple different behaviours can reflect sociability, recent discussion has suggested such components be considered separate personality traits (Koski, 2014). In general, aspects of individuals' sociability fit into two broad categories: gregariousness and relationships with particular individuals. Gregarious tendency does not relate to the specific individuals associated with, and has been quantified in various ways, including preferred group size (Cote, Fogarty, & Sih, 2012) and distance to nearest neighbours (Sibbald, Elston, Smith, & Erhard, 2005). The plasticity of sociability across contexts and situations has been well documented for measures of gregariousness in a range of taxa. In large herbivores, for example, group sizes often vary with predation risk (e.g. Banks, 2001) and habitat structure (e.g. Pays, Benhamou, Helder, & Gerard, 2007).

In contrast to gregariousness, sociability measures such as the quality and numbers of individuals' social relationships (or 'bonds') require consideration of the specific identities of other individuals (Silk, 2007). The strengths of social bonds between pairs of individuals can be measured using a variety of association indices (Cairns & Schwager, 1987). Various metrics of individuals' direct and indirect connectedness within a population can be calculated using social network analysis (Makagon, McCowan, & Mench, 2012; Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordan, 2008), and these have been used as further measures of sociability (e.g. Barocas, Ilany, Koren, Kam, & Geffen, 2011; Jacoby, Busawon, & Sims, 2010; Wey & Blumstein, 2012). Individuals' preferences to associate with or avoid specific others can also be statistically determined (Best, Dwyer, Seddon, & Goldizen, 2014). We know little about how variable these dimensions of sociability are within individuals, or what factors affect such plasticity. However, changes in group density influenced the strengths of social connections among group members in red deer, *Cervus elaphus* (Albon, Staines, Guinness, & Clutton-Brock, 1992), and changes in population size led to alterations in the patterning of social relationships among yellow-bellied marmots, *Marmota flaviventris* (Maldonado-Chaparro, Hubbard, & Blumstein, 2015). There is also some evidence that strengths of social bonds can vary with food availability. Chacma baboon, *Papio hamadryas ursinus*, females formed strong social relationships when food was scarce, but not when food was abundant (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009), suggesting that female social bonds in this species may only be evident when beneficial. Thus, there is some evidence that individuals' social and physical environments can relate to plasticity in their sociability.

Attributes of individuals that vary over the short term, such as reproductive state and body condition, can also relate to plasticity in sociability. This has been reported in microbats, in which female–female associations varied in strength throughout females' reproductive cycles, and associations were stronger during gestation than lactation (Patriquin, Leonard, Broders, & Garroway, 2010). In free-ranging ungulates, the strengths of associations and numbers of associates among females also related to females' reproductive states (Finger, Patison, Heath, & Swain, 2014; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007). However,

most studies that have examined the influence of reproductive state on sociability have been conducted in species in which reproduction is highly synchronous or seasonal, making it difficult to disentangle the effects of seasonal food availability from those of reproductive state. Long- and shorter-term individual-based measures can also interact to further regulate individuals' patterns of sociability, as observed in a facultatively social bird species in which body condition modulated the relationship between personality and grouping tendencies (Öst, Seltmann, & Jaatinen, 2015).

Among social mammals, the degree of spatial and temporal cohesion in a population or group can be described as its fission–fusion dynamics (Aureli et al., 2008). Species that exhibit higher fission–fusion dynamics, in which subgroups frequently change in size and composition and individuals can move freely between such groups, provide an ideal model for studying the combinations of factors that can influence the plasticity of different dimensions of sociability. One such species is the eastern grey kangaroo, *Macropus giganteus*, a large grazing marsupial that feeds in aggregations and exhibits higher fission–fusion dynamics (Jarman, 1994). Some measures of sociability show individual differences that remain stable across years in this species; individual female kangaroos showed high levels of individual consistency in their group sizes and in three social network metrics (strength, affinity and clustering coefficient; Best, Blomberg, & Goldizen, 2015). Nevertheless, these sociability metrics also exhibited considerable plasticity, and other studies suggest that temporally unstable variables, both intrinsic and environmental, may contribute to plasticity in measures of sociability in kangaroos. For example, reproductive state influenced both females' tendencies to feed alone and their likelihoods of being found in groups where adult males were present (Jarman, 1994). Since female kangaroos do not reproduce synchronously (although seasonal breeding peaks have been reported; Stuart-Dick, 1987), this is a species in which the effects of reproductive state on social patterns can be explored separately from confounding effects of food or seasonality.

We aimed to determine for four different dimensions of sociability in female kangaroos (1) the repeatability of each sociability measure and (2) the factors contributing to plasticity in each. The four measures of sociability were (1) females' mean foraging group sizes, (2) mean distances between females and their nearest neighbours in foraging groups, (3) the number of different animals with which females grouped and (4) the number of different nearest neighbours that females had during each month. The first two measures relate to individuals' tendencies to aggregate (their gregariousness), while the final two measures relate to females' propensities to be selective in their choice of grouping patterns and partners. To explore the plasticity of sociability, we tested whether temporally unstable individual states and environmental conditions (and possible interactions among these variables) were related to variation in these measures. Past studies on factors relating to sociability in animals have often used individual-based social metrics derived from social network analysis (e.g. Best et al., 2015; Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011; Wey & Blumstein, 2012). However, social network studies must usually integrate data over substantial time periods. Thus, they cannot be used to investigate how variables that change over shorter time periods relate to plasticity in individuals' sociability.

METHODS

Study Site and Population

Field observations were conducted from January 2010 until December 2014 at Sundown National Park, Queensland, Australia

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