



Strongly bonded individuals prefer to forage together in cooperatively breeding dwarf mongoose groups

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Received: 7 February 2021 / Revised: 6 April 2021 / Accepted: 12 April 2021 / Published online: 30 April 2021
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Abstract

In many social species, group members form strong social bonds. Such strong bonds are well-known to generate long-term fitness benefits, but they are also expected to influence short-term behavioural decisions. Here, we use field observations and an experimental manipulation to investigate whether variation in social-bond strength (as determined from grooming interactions) influences nearest-neighbour choices while foraging in wild dwarf mongooses (*Helogale parvula*). Preferred grooming partnerships (PGPs), representing particularly strong bonds, were found predominately between male–female dyads but among a range of dominance-status dyads. When searching for food, dwarf mongooses with PGPs were more likely than expected by chance to forage close to a preferred grooming partner. Foraging near a strongly bonded groupmate might reduce the predation risk or increase foraging opportunities and the transfer of social information. In addition, there could be stress-reducing benefits, although our field experiment provided no evidence that nearest-neighbour preferences for strongly bonded groupmates were additionally favoured, or indeed disrupted, in the aftermath of a short-term stressful event. Investigating the potential influence of strong social bonds on short-term behavioural decisions with potential fitness consequences is important for our understanding of social interactions and cooperation.

Significance statement

Enduring, close social bonds between individuals provide considerable long-term health and fitness benefits, but are also expected to influence short-term behavioural decisions. We investigated whether social-bond strength (as determined from grooming interactions) influenced foraging decisions in cooperatively breeding dwarf mongoose groups. We found particularly strong social bonds in the form of preferred grooming partnerships in a subset of male–female dyads. Dwarf mongoose foraging decisions were affected by the strength of their social relationships with groupmates: individuals with preferred grooming partners preferred to have these individuals as their nearest neighbours when searching for food. We used a field-based experimental manipulation to investigate whether stressful events impact nearest-neighbour choices, but found no evidence that preferences to forage near strongly bonded groupmates were disrupted or more additionally favoured in the aftermath of a stressful event. Our current work extends understanding of how social bonds can potentially influence within-group behaviour.

Keywords Social bonds · Foraging behaviour · Anti-predator behaviour · Vocal communication · Dwarf mongoose

Introduction

A key characteristic of many animal societies is the existence of strong relationships between group members. Members of stable social groups in humans, non-human primates and other taxa have been shown to possess relationships of different strengths with different groupmates, as a consequence of a variety of factors such as kinship, sex, dominance status and the need for support (Möller et al. 2006; Silk et al. 2006; Cameron et al. 2009; Carter et al. 2009; Napper and Hatchwell 2016). There is

Communicated by B. Voelkl

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convincing evidence that maintaining strong social bonds with other individuals provides considerable long-term health and fitness benefits (reviewed in Silk 2014). For instance, the existence of strong social bonds is related to lower stress levels (Cheney and Seyfarth 2009; Wittig et al. 2016; McFarland et al. 2017), improved reproductive success (Silk et al. 2003; Cameron et al. 2009), longer lifespans (Silk et al. 2010) and lower mortality rates (Ellis et al. 2017). Strong social bonds are also expected to influence short-term decisions, including those relating to foraging and anti-predator behaviour (Ventura et al. 2006; von Bayern et al. 2007; King et al. 2011; Micheletta et al. 2012; Schel et al. 2013; Fuong et al. 2015; Kern and Radford 2016). In this study, we use the cooperatively breeding dwarf mongoose (*Helogale parvula*) to consider the existence of particularly strong social bonds (using long-term grooming interactions), explore the influence of these particularly strong social bonds on foraging behaviour and, finally, investigate whether a short-term stressful event affects bond-related foraging decisions.

Social network analysis quantifies the relationship between each pair of individuals in a group or population, generating association indices to represent the rate at which dyads of individuals interact or associate (Whitehead 2009). Considerable within-group variation in bond strength between different dyads has been revealed through calculation of association indices in a variety of species (e.g. bottlenose dolphins (*Tursiops truncatus*), Möller et al. 2006; baboons (*Papio cynocephalus*), Silk et al. 2006; feral horses (*Equus ferus*), Cameron et al. 2009; eastern grey kangaroos (*Macropus giganteus*), Carter et al. 2009; long-tailed tits (*Aegithalos caudatus*), Napper and Hatchwell 2016). Whilst all values lie on an affiliation continuum, with dyads often having relatively weak bonds (especially in large groups), particularly strong relationships (or ‘preferred partnerships’) can develop between certain individuals (Durrell et al. 2004; Gero et al. 2005; Blasi and Boitani 2014). Preferred partnerships describe dyads with especially high rates of non-random associations; they have sometimes been categorized as the strongest of an individual’s social partners (Goffe et al. 2016; Haunhorst et al. 2017; Goumon et al. 2020) but, more commonly, by association indices above a certain threshold (Durrell et al. 2004; Gero et al. 2005; Blasi and Boitani 2014). For example, in bottlenose dolphins (Gero et al. 2005; Blasi and Boitani 2014), Atlantic spotted dolphins (*Stenella frontalis*; Elliser and Herzing 2014), short-finned pilot whales (*Globicephala macrorhynchus*; Mahaffy et al. 2015), benthic sharks (*Orectolobus maculatus*; Armansin et al. 2016) and domestic pigs (*Sus scrofa domesticus*; Durrell et al. 2004; Goumon et al. 2020), preferred partnerships were categorized as dyads with an association index more than twice the population mean. Most works have considered fission–fusion societies (Gero et al. 2005; Blasi and Boitani 2014); to the best

of our knowledge, no previous studies have examined the presence of particularly strong relationships in cooperatively breeding species in the wild.

In many social species, individuals search for food independently but in a loose aggregation (e.g. pied babblers (*Turdoides bicolor*), Radford and Ridley 2008; baboons, King et al. 2011; meerkats (*Suricata suricatta*), Gall and Manser 2017; dwarf mongooses, Kern and Radford 2018), requiring continuous decisions about which groupmates to be in the vicinity of while foraging. Individuals may benefit from foraging close to groupmates with whom they share strong social bonds if, for example, this minimizes foraging competition or enhances the likelihood of food sharing (Ventura et al. 2006; von Bayern et al. 2007; King et al. 2011; Heesen et al. 2014; Dale et al. 2017; Samuni et al. 2018), improves access to social information (Aplin et al. 2012; Claidière et al. 2013), decreases predation risk (Micheletta et al. 2012; Schel et al. 2013; Fuong et al. 2015; Kern and Radford 2016) or reduces general stress levels (Cohen and Wills 1985; Wittig et al. 2008, 2016). While spatial proximity can be used to create association networks and describe social structure/organization, there remains contention over the suitability of comparing networks constructed using different data collection techniques (Machanda et al. 2013; Castles et al. 2014; Carter et al. 2015; Canteloup et al. 2020). In particular, where physical contact or behavioural interactions (e.g. grooming) can be easily observed and quantified, comparisons with networks constructed using spatial associations as a proxy for social interactions may not be helpful or justified (Machanda et al. 2013; Castles et al. 2014; Carter et al. 2015).

While individuals often choose to forage close to strongly bonded groupmates, they do not do so all of the time (Ventura et al. 2006; King et al. 2011). Instead, foragers must balance assorted costs, such as patch depletion and risk of kleptoparasitism (Radford and Ridley 2008), with the benefits mentioned above (e.g. food sharing, social information provision, anti-predator behaviour and stress reduction). The benefits provided by the close proximity of strongly bonded groupmates may be more likely to outweigh associated costs in the aftermath of short-term stressful events, such as intergroup contests (Radford et al. 2016) or predator attacks (Clinchy et al. 2012). For example, social information about predation risk can be shared more effectively between strongly bonded individuals (Aplin et al. 2012; Schel et al. 2013; Kulahci et al. 2016; Blumstein et al. 2017); strongly bonded individuals are more likely to assist one another in collective defense against intruders or predators (Micheletta et al. 2012; Kern and Radford 2016), and the presence of close associates can reduce stress (Young et al. 2014; Wittig et al. 2016). Alternatively, stressful events might disrupt natural foraging patterns, with groupmates less likely to have a strongly bonded groupmate as their nearest neighbour in the immediate aftermath. If so, short-term

stressful events might temporarily negate any advantages conferred by nearest-neighbour choices, which may be particularly costly if those benefits are predator-related (Micheletta et al. 2012; Schel et al. 2013; Fuong et al. 2015; Kern and Radford 2016).

Here, we investigate whether variation in social-bond strength influences nearest-neighbour choices while foraging in a wild population of dwarf mongooses; the study population has been habituated close to human presence, facilitating detailed observations and field-based manipulations (Kern and Radford 2013, 2014, 2016, 2017, 2018). Dwarf mongooses are cooperative breeders living in small stable groups (mean \pm SE group size = 8 ± 0.2 adult individuals, range 3–17; 2011–2019 Dwarf Mongoose Research Project (DMRP), unpub. data). A dominant pair monopolizes reproduction, with females holding tenure for a mean of 640 days and males for 590 days; dominants are generally replaced by the next oldest and heaviest individual within the group (DMRP unpub. data). Both related and unrelated subordinates of both sexes contribute to various cooperative behaviours, including helping to rear offspring, sentinel behaviour (raised guarding) and territorial defense (Rood 1980; Christensen et al. 2016; Kern and Radford 2016). Group members also engage in regular allogrooming (hereafter grooming), the majority of which occurs at the sleeping refuge before and after daily foraging (Kern and Radford 2018). Dwarf mongooses spend daylight hours foraging individually in a loose group, digging for predominantly invertebrate prey (Rasa 1977), when they are vulnerable to a variety of terrestrial and aerial predators (Collier et al. 2017). Group members can forage within 50 cm of one another but are on average 2.5 m from their nearest neighbour (DMRP unpub. data).

Here, we first use naturally observed grooming interactions to calculate within-group social networks and, then, to determine the occurrence of preferred grooming partnerships (PGPs) among groupmates. We expect social bonds to be particularly strong between the dominant pair; they are the only group members guaranteed to reproduce and are instrumental to group stability (dominance changes are often associated with periods of group instability, DMRP unpub. data). Second, we use observations of natural behaviour to examine the choice of foraging partners with reference to the grooming network, asking whether variation in social-bond strength, and the presence of particularly strong social bonds in particular, affects the choice of nearest neighbours while foraging. We expect individuals with particularly strong social bonds to show nearest-neighbour preferences for these individuals. Finally, we use a field-based experiment to test how foraging choices are affected following a likely stressful event (a potential predator attack). We expect that preferred foraging partners will be favoured even more strongly if their close presence reduces stress or that there

will be disruption to preferred foraging relationships in the immediate aftermath of a stressful event.

Material and methods

Study site and population

Work was conducted on a population of wild dwarf mongooses on Sorabi Rock Lodge, Limpopo Province, South Africa (24° 11' S, 30° 46' E). Data were collected from 14 groups (mean number of adults = 7; range 4–12) habituated to the close presence of human observers (< 5 m); individuals were identifiable from small blonde dye marks (Wella UK Ltd, Surrey, UK) applied to the fur (Kern and Radford 2013, 2014, 2016). The population has been monitored since 2011, and thus the age of most individuals is known; individuals can be sexed through observations of ano-genital grooming. Adult group members (> 12 months old) were classified as either 'dominant' (single male and female breeding pair per group) or 'subordinate' (the remaining individuals) (as in Kern and Radford 2013, 2014, 2016). The dominant pair could be easily identified through observations of aggression, feeding displacement, scent marking, greeting behaviour and breeding activity (Rasa 1977). They are also considerably heavier (approx. 15 g) than their groupmates, and produce close calls at a noticeably lower pitch (DMRP unpub. data). In the present study, we chose to consider only grooming and foraging data collected during the non-breeding season (April–October), for two main reasons. First, given the complexities associated with dynamic social network analysis, we chose to use only stable periods where there was no change in group membership. As dispersal tends to take place in the immediate run-up to and during the breeding season (Kern and Radford 2017), stable periods predominately occur during the non-breeding season. Second, during the breeding season, foraging behaviour is likely disrupted by periods of intense mate guarding between the dominant pair, and by the weeks of babysitting where some group members remain at the sleeping refuge with young pups, while the rest of the group are away foraging (Rasa 1977; Rood 1980). Thus, to ensure all group members were foraging at any given time (and thus all periods were comparable), we chose to use only non-breeding periods.

Occurrence of particularly strong social bonds

Grooming data were collected from all-occurrence sampling between 2015 and 2019, with the identity of grooming partners recorded during all observed grooming bouts lasting longer than 5 s that occurred between individuals aged 12 months and older. We focused on adults because pup survival is low and few individuals are recruited to

1 year of age (DMRP unpub data); thus, when including individuals < 12 months old, group composition changes regularly. Bouts were considered to have ended if 10 s elapsed without any grooming. Social network analysis was confined to one stable 4-month winter period per group (N = 14 groups) when there was no change in membership; 4 months was chosen for consistency as the shortest stable period with sufficient grooming data observed across all groups (as in Kern and Radford 2018; 5,225 grooming bouts in total, mean \pm standard deviation (SD) grooming bouts per group = 373 ± 130 , range = 161–627; Table 1). Each year, between four and eight different groups were under observation. If groups were followed for multiple years and multiple stable 4-month periods were available, we used the period with the largest grooming sample size for analysis.

To calculate the strength of social bonds between group members, weighted association matrices were constructed for each 4-month period using the Simple Ratio Index in the program SOCPROG 2.4 (Whitehead 2009; as in Kern and Radford 2018). This represents the proportion of times a dyad was observed grooming as a function of their combined number of observations (Whitehead 2009). Association indices represent the strength of the relationship between individuals in a dyad, and values typically range from 0 (i.e. the individuals were never observed grooming together) to 1 (i.e. the individuals were always seen grooming together). Matrices were treated as weighted (i.e. the rate at which a dyad interacted was calculated, rather than simply the presence/absence of an interaction), but undirected as > 95% grooming bouts were reciprocated (i.e. both partners groomed each other within a single bout). Data were not filtered (i.e. removing relationships with fewer than x observations) as group composition was stable for the analysis period and groups were visited regularly. Therefore, little

data for a dyad is likely representative of a weak connection between individuals that rarely interact.

To determine whether dwarf mongooses were simply grooming at random, matrices were compared with randomly permuted association matrices following Whitehead's (2009) modification of the Bedjer et al. (1998) test in SOCPROG (Best et al. 2013; Napper and Hatchwell 2016; Rose and Croft 2017). For each group, permutations were run 2000 times over 2000 trial flips, after which P values stabilized to within 0.01. Dyads were flipped within sampling periods, maintaining the number of associates of each individual as well as the total number of associations within each sampling period (Bedjer et al. 1998; Whitehead 2009). The coefficient of variation (CV) of the association indices was used as the test statistic where an observed value significantly higher than the randomized values represents the presence of non-random associations. Significantly higher standard deviation (SD) and CV of real data compared to random data indicate preferred associations. If the real value fell within the top or bottom 2.5% of the random distribution ($P > 0.975$ or $P < 0.025$), we rejected the null hypothesis that the real value could have arisen by chance (Napper and Hatchwell 2016). In addition, we examined how heterogeneous the social structure was and determined whether there was sufficient power to describe the social structure (as in Best et al. 2013). To determine the degree of heterogeneity in intragroup relationships, social differentiation was calculated in SOCPROG using the coefficient of variation of the association indices (S); values of S greater than 0.5 represent a well-differentiated social system, i.e. large disparity in the amount of time different dyads spend together (Whitehead 2009; Best et al. 2013; Elliser and Herzing 2014; Rose 2019). To determine whether there was sufficient power to describe the social structure, power was assessed using

Table 1 Number of individuals (total and by sex; *F* female, *M* male), sampling periods (days) and grooming records used for analyses in each grooming network, alongside resulting grooming-association indices and number of preferred grooming partners (PGPs). PGPs were dyads whose grooming-association index was more than twice the mean grooming-association index of their group

Group	Group size	F/M	Number of sampling periods	Number of grooming records	Mean grooming association index	Number of PGPs
GA	4	2/2	28	161	0.37	0
GB	5	2/3	50	627	0.35	1
GC	6	3/3	33	263	0.23	2
GD	6	1/5	30	380	0.28	1
GE	6	4/2	41	446	0.27	2
GF	6	4/2	30	364	0.25	2
GG	6	3/3	34	345	0.26	2
GH	7	3/4	27	477	0.19	2
GI	7	3/4	35	344	0.18	4
GJ	7	4/3	19	295	0.24	4
GK	7	4/3	31	614	0.22	2
GL	9	4/5	27	314	0.15	3
GM	10	3/7	45	340	0.11	5
GN	12	6/6	26	255	0.09	6

the correlation between the true and estimated association indices; values near to 1 indicate excellent representation of social structure and values around 0.4 indicate moderate representation (Whitehead 2009; Best et al. 2013). The maximum likelihood method was used for both tests. Finally, to identify whether social preferences were influenced by the sex or dominance status of individuals, a MRQAP test (Multiple Regression Quadratic Alignment Procedure; Dekker et al. 2007) was conducted in SOCPROG (Whitehead 2009). The MRQAP is an extension of the Mantel test that enables a dependent matrix to be regressed against multiple independent matrices. Here, the matrix of dyadic association indices was used as the dependent matrix, and the two independent matrices consisted of group members' attribute data (sex and dominance status) converted into an association measure (Rose 2019).

The occurrence of dyads with particularly strong social bonds, or 'preferred grooming partnerships' (PGPs), was then determined. Grooming-association indices for all dyads in the group were compared to the mean grooming-association index for each group. Individuals were defined as having a PGP when their dyadic grooming-association index was more than twice the mean grooming-association index of their group, a method believed to represent 'meaningful' associations (as in Durrell et al. 2004; Gero et al. 2005; López and Shirai 2008; Pace et al. 2012; Wiszniewski et al. 2012; Blasi and Boitani 2014; Elliser and Herzing 2014; Mahaffy et al. 2015; Armansin et al. 2016; Genov et al. 2019; Goumon et al. 2020). A PGP therefore indicates a dyad which associated at least twice as much as expected if grooming partners were entirely random. Dyads with grooming-association indices below this threshold were classified as 'non-preferred grooming partnerships' (NPGPs).

Influence of particularly strong social bonds on foraging behaviour

To determine if individuals exhibit natural foraging preferences related to social-bond strength, observational data were collected between 2015 and 2019; analysis focused on the same 4-month periods when PGPs and NPGPs were calculated from grooming observations (see above). Scan samples were carried out every 30 min once groups had left the overnight refuge to begin foraging until they returned to an overnight refuge at the end of the day (Kern and Radford 2016). During each scan, the identity of the single nearest foraging neighbour for each visible group member was recorded. When a dyad was each other's nearest neighbours, A's nearest neighbour was recorded as B and B's as A. As 2.5 m is the mean nearest-neighbour distance ($N=48,900$ foraging scans), we analyzed occurrences when the nearest foraging individual was < 2.5 m away. One group was discarded due to a lack of PGPs and subsequent analyses

therefore focused on grooming networks from 13 groups. In total, 4390 nearest-neighbour identities were recorded from the 13 groups (mean \pm SD nearest-neighbour identities per group = 337 ± 111 , range = 191–600).

Wilcoxon signed-rank tests were used to compare observed and expected values from the observational foraging data. First, to determine whether individuals generally preferred to have groupmates with which they are more strongly bonded as their nearest neighbours, data from all group members were used to examine whether the grooming-association indices of foraging nearest neighbours were higher than expected by chance. Expected scores were calculated by multiplying an individual's mean dyadic grooming-association index (i.e. the average of their dyadic grooming-association indices with all group members) by the number of foraging scans in which they were recorded ($N=94$ individuals, 13 groups, mean \pm SD foraging scans per individual = 47 ± 40). For example, if individual A was recorded in 50 foraging scans and had a mean grooming-association index of 0.16, it would receive an expected score of 8. Observed scores were calculated by summing the dyadic grooming-association indices for all occasions that an individual had a recorded nearest neighbour. For example, individual A's observed score would be calculated by summing the dyadic grooming-association indices of individual A and their nearest neighbour in the 50 scans.

Next, to examine the potential importance of PGPs in driving the discovered nearest-neighbour preferences, the above analysis was repeated separately on two subsets of data: those individuals with only NPGPs ($N=38$ individuals) and those individuals with at least one PGP ($N=56$ individuals). Finally, for the subset of individuals that had at least one PGP ($N=56$ individuals), the observed proportion of foraging scans in which their nearest neighbour was a preferred grooming partner was compared with that expected by chance. Expected proportions were taken as the proportion of an individual's total dyads that were PGPs. For example, each individual in a group of seven belongs to six dyads; therefore, if individual A has two PGPs, they would be expected by chance to forage nearest to a PGP in a third of all scans. All analyses were performed using R version 3.2.4 (R Development Core Team 2012); all tests were two-tailed and were considered significant at $P < 0.05$.

Effect of a short-term stressful event on bond-related foraging decisions

To investigate experimentally whether a likely stressful event affects nearest-neighbour choices, five groups were exposed to two treatments between June and October 2017. In the 'stressful' treatment, a conspecific aerial alarm call from a non-group member was broadcast, warning of a potential predatory attack and causing group members

to run for cover (Collier et al. 2017). The ‘non-stressful’ (control) treatment involved summoning the mongooses to the observer with a ‘yip-yip’ call (similar in duration to an aerial alarm call). This is an attractive call with a strong positive valence causing individuals to pause foraging and run towards the observer (usually given by human observers in conjunction with the presentation of hard-boiled egg used to entice individuals onto weighing scales during each data-collection session as part of the long-term Dwarf Mongoose Research Project). In this case, however, the ‘yip-yip’ call was given without the presentation of any egg to avoid foraging competition or alteration of state. The aim of the control manipulation was to disrupt current foraging-partner identity but without causing any likely stress.

For use in stressful trial playbacks, alarm calls given to flying raptors were recorded opportunistically from 0.5 to 10 m during behavioural observations of adult individuals at a sampling rate of 44.1 kHz with a 16-bit resolution onto a SanDisk SD card (SanDisk, Milpitas, CA, USA). Recordings were made using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a hand-held highly directional Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Eight 10-s playback tracks, consisting of a single unmanipulated aerial alarm call (approx. 4-s duration) placed in the middle of ambient sound (recorded from approximately the center of the territory of the focal group) were constructed using Raven Pro (version 1.5, The Cornell Laboratory of Ornithology, NY, USA); tracks did not include any other vocalizations from dwarf mongooses or other species. Tracks were broadcast from an mp3 player (Apple Inc., Cupertino, CA, USA) connected to a single portable speaker (Tevo, South Africa) at ground level. Playback amplitude was standardized according to the amplitude of naturally occurring aerial alarm calls (55-dB SPLA at 2 m) using a HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West Yorkshire, UK). Different playback tracks were used for repeat trials to the same group to ensure no group heard the same alarm call more than once.

Experiments were paired, with the two trials (experimental and control) in a pair conducted on the same day, at least 30 min apart. To maximize observations and control for potential daily variation, multiple pairs of experimental trials were run ($N=21$) in the five groups under study during 2017 (median per group=3, range 1–4). Repeats to the same group were separated by at least 48 h. Treatment order was counterbalanced across pairs of trials to the same group and across groups. Trials were conducted when the majority of group members were foraging and visible, and when no natural alarm calls had been given for at least 30 min. In both treatments, the identity of the nearest foraging neighbour

for each visible individual was noted immediately before the acoustic stimulus began (‘pre-manipulation’), and again once the group had resumed foraging following foraging disruption (‘post-manipulation’). Given the acoustic nature of our trials, it was not possible to conduct experiments blind to treatment; however, the observer did not know the identity of PGPs/NPGPs within the group.

The experimental data were used to examine differences in foraging choices between stressful and non-stressful treatments. First, the difference in mean observed and expected post-manipulation grooming-association indices was calculated for each individual and a Wilcoxon signed-ranks test used to compare the two treatments ($N=24$ individuals, five groups, mean \pm SD foraging scans per individual = 4 ± 4). Second, the change in mean observed grooming-association indices from pre-manipulation to post-manipulation was also calculated for each individual and a Wilcoxon signed-ranks test used to compare the two treatments ($N=24$ individuals, five groups, mean \pm SD foraging scans per individual = 9 ± 8.5). Only individuals for whom pre- and post-manipulation data were available in control and experimental trials were used.

Results

Occurrence of particularly strong social bonds

In all 14 groups, dwarf mongoose grooming networks had social differentiation values > 0.5 (Table 2), indicating highly differentiated grooming behaviour. The correlation between the true and estimated association indices was > 0.7 in all groups (Table 2), indicating sufficient power to draw conclusions on the social structure of the population. The presence of non-random associations in the network was further supported by permutation testing: in all groups, the CV and SD of observed association indices were lower than those of at least 99.5% of random permutations (Table 2). Sex was a significant predictor of grooming associations in eight of 14 groups (MRQAP test: $P < 0.05$; Table 2), with stronger grooming associations exhibited between opposite-sex pairs. Dominance status was not a significant predictor of grooming associations (MRQAP test: $P > 0.05$; Table 2).

PGPs were found in 13 of the 14 groups (median number of PGPs per group = 2, range = 0–6; Table 1; Fig. 1a). Of a total 322 dyads across the 14 groups, 36 (11%) were PGPs; 56 individuals were part of at least one PGP (median number of PGPs per individual = 1, range = 0–3), while 42 individuals had only NPGPs. The lack of any PGPs in one group may have been an artifact of group size: this group had only four members, giving it the largest mean grooming association-index, and while several dyads had high association indices they

Table 2 Output from social network analysis of grooming matrices. All grooming matrices were socially differentiated ($S > 0.5$; S , social differentiation) and good representations of true social structure (correlation between real and estimated grooming matrices > 0.6). SD (standard deviation) and CV (coefficient of variation) from permutation tests comparing real matrices with 2000 randomly permuted matrices. MRQAP tests comparing association indices and sex, and association indices and dominance status. Significant outputs shown in bold

Group	S	Correlation between the true and estimated association indices	SD	CV	MRQAP sex	MRQAP status
GA	0.549	0.910	$P=0.0010$	$P=0.0010$	$P=0.1060$	NA
GB	0.606	0.930	$P<0.0001$	$P<0.0001$	$P=0.0820$	$P=0.7260$
GC	0.816	0.904	$P<0.0001$	$P<0.0001$	$P=0.0652$	$P=0.9758$
GD	0.547	0.865	$P=0.0005$	$P<0.0001$	$P=0.0350$	$P=0.9500$
GE	0.712	0.971	$P=0.0005$	$P=0.0005$	$P=0.2616$	$P=0.3604$
GF	0.582	0.826	$P=0.0020$	$P=0.0025$	$P=0.0994$	$P=0.3980$
GG	0.560	0.825	$P<0.0001$	$P=0.0005$	$P=0.1210$	$P=0.8372$
GH	0.783	0.867	$P=0.0035$	$P=0.0030$	$P=0.0189$	$P=0.4208$
GI	0.778	0.778	$P=0.0005$	$P=0.0005$	$P=0.0080$	$P=0.6700$
GJ	0.707	0.862	$P=0.0005$	$P<0.0001$	$P=0.0080$	$P=0.4760$
GK	0.504	0.761	$P=0.0005$	$P<0.0001$	$P=0.0120$	$P=0.4460$
GL	0.685	0.735	$P=0.0005$	$P<0.0001$	$P=0.0072$	$P=0.3704$
GM	0.843	0.706	$P<0.0001$	$P<0.0001$	$P=0.0222$	$P=0.9814$
GN	0.607	0.658	$P=0.0050$	$P=0.0040$	$P=0.0022$	$P=0.9180$

did not reach the level required as twice the mean. PGPs were almost exclusively found among opposite-sex dyads, with 97% PGPs (35/36) between male and female group members (Fig. 1b). Examining only opposite-sex dyads ($N = 174$), PGPs were also more likely among certain dominance-status dyads (Fig. 1c), with 79% (11 out of 14) of dominant–dominant dyads being PGPs, 11% (8 out of 71) of dominant–subordinate dyads and 19% (17 out of 89) of subordinate–subordinate dyads (Fig. 1c).

Influence of particularly strong social bonds on foraging behaviour

Social-bond strength, calculated with reference to grooming relationships, influenced nearest-neighbour choice while foraging. When considering the observational foraging data from all individuals, the grooming-association indices of nearest neighbours were significantly higher than expected by chance (Wilcoxon signed-rank test: $V = 3486$, $N = 94$, $P < 0.001$). This overall result was driven by individuals

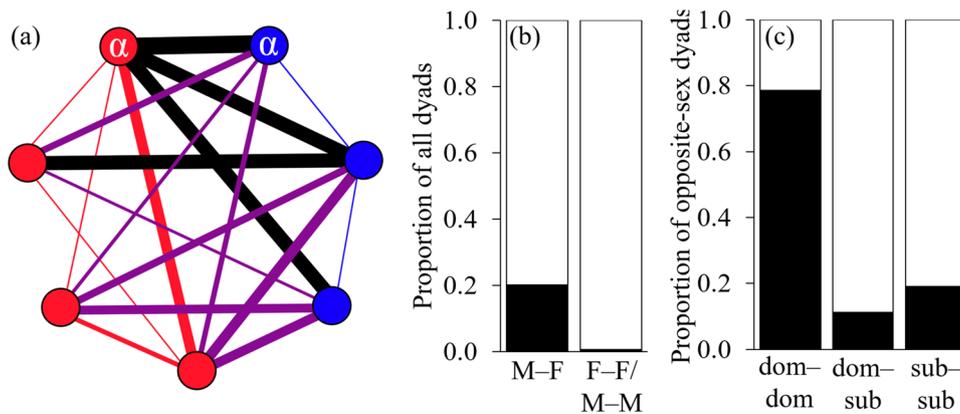


Fig. 1 Within-group grooming relationships. **a** An example group’s grooming network. Node color denotes sex (female=red, male=blue), α denotes dominant pair. Line thickness between individuals is proportional to the strength of the dyadic grooming association, line color denotes the type of relationship (black=preferred grooming partners, i.e. dyadic grooming-association index more than twice the mean grooming-association index of the group; pur-

ple = male–female, red = female–female, blue = male–male). Network diagram constructed using Gephi 0.9 (Bastian and Heymann 2010). PGPs (black bars) were more likely to be found **b** in opposite-sex dyads ($N=35$ of 174) than same-sex dyads ($N=1$ of 148), and **c** in dominant–dominant dyads ($N=11$ of 14) than dominant–subordinate dyads ($N=8$ of 71) or subordinate–subordinate dyads ($N=17$ of 89)

belonging to PGPs: whilst the dyadic social-bond strengths (i.e. grooming-association indices) of nearest neighbours for individuals that had only NPGPs were not significantly different from expected ($V=387$, $N=38$, $P=0.597$; Fig. 2a), the observed nearest-neighbour social-bond strengths for those individuals with at least one PGP were significantly higher than expected ($V=137$, $N=56$, $P<0.001$; Fig. 2a). Individuals with at least one PGP foraged nearest to a preferred grooming partner significantly more often than expected ($V=259$, $N=56$, $P<0.001$; Fig. 2b), and were recorded <2.5 m from a PGP in 32% of scans compared to 21% scans expected by chance.

Effect of a short-term stressful event on bond-related foraging decisions

There was no evidence that the short-term stressful manipulation (alarm-call playback) affected nearest-neighbour choices either positively or negatively. Using only post-manipulation data, the differences in mean observed and expected social-bond strength (i.e. grooming-association indices) of nearest neighbours did not differ significantly between treatments (Wilcoxon signed-rank test: $V=165$, $N=24$, $P=0.110$). Similarly, there was no significant difference between non-stressful and stressful treatments in the

change in mean observed social-bond strength of nearest-neighbours from pre-manipulation to post-manipulation ($V=117$, $N=24$, $P=0.972$).

Discussion

Our results detail the existence of particularly strong social bonds, in the form of preferred grooming partnerships (PGPs), between a subset of male and female dwarf mongoose group members. We demonstrate that foraging nearest-neighbour choices are affected by the strength of within-group social relationships: individuals with PGPs preferred to forage near to those groupmates. However, our field experiment provided no evidence that these nearest-neighbour preferences are more strongly favoured or disrupted in the aftermath of a stressful event. In combination with previous work, it is clear that allogrooming behaviour helps to establish and maintain within-group social bonds in dwarf mongooses, and these strongly influence short-term decisions relating to both anti-predator responses (Kern and Radford 2016) and foraging behaviour (this study).

PGPs were found in the majority (13 out of 14) of the studied dwarf mongoose groups, with the lack of any PGPs in one group likely explained by its small size; our chosen

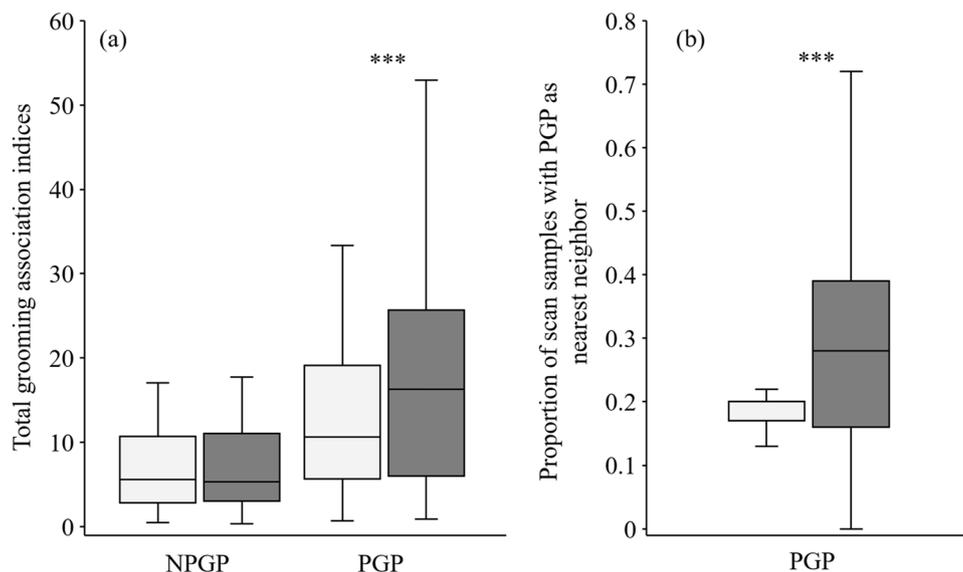


Fig. 2 Individuals with preferred grooming partnerships prefer to forage with those individuals in baseline conditions. In natural foraging situations, **a** individuals with preferred grooming partnerships (PGPs) were more likely than expected to forage closest to groupmates with whom they shared higher grooming-association indices, whilst individuals with no preferred grooming partnerships (NPGPs) were not ($N=94$ individuals, 13 groups). Expected values (pale boxes) were calculated by multiplying the number of scans an individual was seen in with its mean grooming association index, observed values (dark boxes) were calculated by summing the dyadic grooming-association

indices for all scans that an individual had a recorded nearest neighbour. **b** Individuals with PGPs foraged nearest to a preferred grooming partner more often than expected. Expected proportions were taken as the proportion of an individual's total dyads that were PGPs, observed values were calculated as the proportion of foraging scans in which their nearest neighbour was a preferred grooming partner. Boxplots show median values (horizontal lines), and interquartile range between the 25% and 75% quartiles (upper and lower box limits respectively). Whiskers show data range of 1.5 times the interquartile range from the 25% and 75% quartiles, ***indicates $P<0.001$

method of identifying PGPs deals well with larger groups but has limitations for small groups, thus caution is needed when drawing conclusions in groups of four and below. Similar, disproportionately strong social bonds have been described in other species (baboons, Silk et al. 2006; feral horses, Cameron et al. 2009; eastern grey kangaroos, Carter et al. 2009; bottlenose dolphins, Blasi and Boitani 2014; short-finned pilot whales, Mahaffy et al. 2015; Guinea baboons (*Papio papio*), Goffe et al. 2016; flamingos (Phoenicopteridae), Rose and Croft 2017; chimpanzees (*Pan troglodytes*), Samuni et al. 2018; pigs, Goumon et al. 2020), and their long-term benefits well-documented (reviewed in Silk 2014). Unusually, dwarf mongoose PGPs occurred almost exclusively between males and females. This differs from another social mongoose, the meerkat, where grooming relationships are predominantly between same-sex individuals (Kutsukake and Clutton-Brock 2010). Prevalent opposite-sex grooming has been reported in some primate species (Palombit et al. 1997; Cooper and Bernstein 2000; Silk et al. 2003; Lemasson et al. 2008; Weyher et al. 2014) but, for the majority, grooming is also largely a same-sex interaction outside of the breeding season (Cooper and Bernstein 2000; Lemasson et al. 2008; Goffe et al. 2016).

While dwarf mongoose PGPs were found in some opposite-sex dominant–subordinate and subordinate–subordinate dyads, the relative likelihood of occurrence was higher between a group's dominant male and female pair. This is in line with previous work on meerkats, where grooming was most common between a group's dominant pair (Kutsukake and Clutton-Brock 2010) and supports the sexual bond hypothesis, where grooming functions to maintain sexual pair bonds between dominant individuals. The advantages of stable pair bonds between breeding partners have been well documented in monogamous species (Forslund and Larsson 1991), and recent work on pied babblers demonstrated that breeding success similarly increases with pair tenure in a cooperatively breeding species (Wiley and Ridley 2018). The adaptive value of PGPs between opposite-sex dominant–subordinate and subordinate–subordinate dyads in dwarf mongoose remains unclear. Research generally attributes sex-specific preferences in grooming relationships to sex-specific patterns of dispersal and resulting kinship differentials (Weyher et al. 2014). However, dispersal in dwarf mongooses is male-biased (Kern and Radford 2017), thus kin-based PGPs would be expected along same-sex not opposite-sex lines. Opposite-sex grooming relationships have also been attributed to reproductive strategy, as a way to improve mating chances (Gumert 2007) or access paternal care (Huchard et al. 2010). Although dwarf mongooses have high reproductive skew and only the dominant pairs are guaranteed to reproduce, high-ranking subordinates are known to mate with both dominants and other high-ranking subordinates during periods of synchronized estrus (Rood

1980). Opposite-sex PGPs might, therefore, be a tactic to improve mating opportunities in dwarf mongooses, but as grooming was examined during the non-breeding season, any access to mating rights would only take place in the future. Alternatively, where grooming is used as a pacifying or submissive strategy, sex-specific grooming preferences could relate to the distribution of intra-group aggression (Kutsukake and Clutton-Brock 2006). Here, however, this also seems unlikely, as dwarf mongoose groups are characterized by low levels of internal aggression and compared to other social mongooses, eviction is conspicuously absent (DMRP unpub. data). Additional long-term analysis is needed to establish whether matings by group members other than the dominant pair are more likely among PGPs, and whether PGPs persist between seasons, across years and following changes in group membership and dominance status.

Our finding that strongly bonded individuals are more likely than those with weaker bonds to show preferred foraging associations matches previous observational work on Japanese macaques (*Macaca fuscata*) and baboons (Ventura et al. 2006; King et al. 2011). Whereas the primate work found that there was a general tendency for all individuals to exhibit preferred foraging associations with those with whom they are more strongly bonded (Ventura et al. 2006; King et al. 2011), our results show this to be true of only a subset of individuals in dwarf mongoose groups—those with PGPs; group members with only NPGPs did not select nearest neighbours with whom they shared relatively stronger social bonds. Given that the dominant pair often formed a PGP, one potential explanation for the demonstrated nearest-neighbour choices could be social monitoring. Foraging close to each other could be a mechanism by which dominant males seek to prevent extrapair mating by dominant females. While we collected data for this study during the non-breeding season, purposely to avoid any complications of mate guarding, it is possible that relevant dyads maintain a preferred foraging association year-round. However, since some PGPs were also found between dominants and subordinates or between two subordinates, a mate-guarding or social-monitoring explanation is unlikely to be the main reason for choosing to forage nearest to a PGP.

Instead, foraging next to PGPs may accentuate known advantages of group living if, for example, acquisition of social information about foraging opportunities or predation risk is improved between strongly bonded individuals (Aplin et al. 2012; Schel et al. 2013; Kulahci et al. 2016; Blumstein et al. 2017). Individuals with stronger bonds may also be more likely to assist one another in collective defense against predators; in dwarf mongooses, groupmates are more likely to respond to the snake-mobbing recruitment calls of close associates than those of individuals to whom they are weakly bonded (Kern and Radford 2016). In addition, the presence

of close associates can alleviate stress (Young et al. 2014; Wittig et al. 2016). Alternatively, or additionally, observed foraging patterns may lessen known disadvantages of group living. Close associates may be more tolerant of one another during foraging compared to other group members; they may be more likely to share food items or foraging patches, engage in fewer aggressive interactions whilst feeding, and be less likely to steal food (Ha et al. 2003; Ventura et al. 2006; King et al. 2008, 2011; Heesen et al. 2014; Dale et al. 2017; Samuni et al. 2018). In vervet monkeys (*Chlorocebus pygerythrus*), for example, individuals that increased investment in grooming gained access to better foraging opportunities (Fruteau et al. 2009). Although dwarf mongoose society is characterized by low levels of intragroup aggression in general (Rood 1983), foraging displacements and theft do occur, especially in the winter months when food is scarce (Sharpe et al. 2013). Experimental work is now needed to determine whether dwarf mongooses that are members of PGPs gain benefits, such as an increased food intake or social information, or reduce time and energy costs associated with aggression and kleptoparasitism, by foraging in close association with one another.

Our experimental results indicate that, whatever the benefits arising from such nearest-neighbour choices, stressful events (at least an alarm call) do not lead to their disruption. Since stress can negatively affect attention, information-processing and decision-making (Mendl 1999; Starcke and Brand 2012), suboptimal foraging choices might have been expected in the aftermath. However, we did not see any change in nearest-neighbour choices following an alarm-call playback compared to our control treatment, both of which resulted in temporary suspension of foraging as the dwarf mongooses moved either towards an observer or to cover. There was also no evidence for an even greater preference to forage with a preferred grooming partner when individuals returned to foraging following an alarm-call playback compared to our control treatment. Since stress can be alleviated by the presence of close affiliates (Young et al. 2014; Wittig et al. 2016), including during particular events (Wittig et al. 2008), a greater association with preferred grooming partners might have been expected in the aftermath. It is possible that a single alarm call was not sufficiently stressful to generate differences in foraging-partner choice, especially as there are likely other factors such as spatial position within the foraging group (King et al. 2011; Tkaczynski et al. 2014), satiation level (Kern and Radford 2017) and individual personality (Dammhahn and Almeling 2012) that play a role. It is also possible that differences in foraging patterns would have become apparent if we had collected data beyond the initial return to foraging.

Our current work extends understanding of how social bonds can potentially influence within-group behaviour. As in many other mammalian species, individual dwarf mongooses

show considerable variation in the strength of their social relationships with different group members, including having strongly preferred grooming partners. It is increasingly apparent that similar social bonds occur across animal groups, including birds and fish (e.g. von Bayern et al. 2007; Carter et al. 2009; Kelley et al. 2011; Aplin et al. 2012; Armansin et al. 2016; Hasenjager and Dugatkin 2017), and so this is likely a widespread occurrence in the natural world. Studies have also empirically demonstrated that external conditions can themselves influence social bonds and network structure (Kelley et al. 2011; Hasenjager and Dugatkin 2017), so there is likely a dynamic interaction between behaviour and relationship strength. While the long-term benefits of strong social bonds are well-established, especially in primates, investigating the potential influence on short-term behavioural decisions with potential fitness consequences is important to broaden our understanding of social interactions and the evolution of cooperation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-03025-0>.

Acknowledgements We thank B. Rouwhorst and H. Yeates for access to their land, Amy Sibun for pilot work, and 24 research assistants for their invaluable assistance with observational data collection. We thank two anonymous reviewers for their exceedingly helpful comments.

Author contribution Both authors conceived the study. JMK collected the data and analyzed the data with advice from ANR. Both authors interpreted the data and wrote the manuscript.

Funding This research was supported by a University of Bristol Science Faculty Studentship (to J.M.K.) and a European Research Council Consolidator Grant 682253 (to A.N.R.).

Data availability The datasets analyzed in this study are available as part of the electronic supplementary material.

Declarations

Ethics approval All applicable national and institutional guidelines for the use of animals were followed. Work was conducted under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number 001-CPM403-00,013), the Ethical Review Group of the University of Bristol, UK, and the Ethical Committee of Pretoria University, South Africa.

Consent for publication All authors have approved the manuscript and agree with its submission to *Behavioral Ecology and Sociobiology*.

Conflict of interest The authors declare no competing interest.

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