



The role of anointing in robust capuchin monkey, *Sapajus apella*, social dynamics

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Anointing is a behaviour in which animals apply pungent-smelling materials over their bodies. It can be done individually or socially in contact with others. Social anointing can provide coverage of body parts inaccessible to the individual, consistent with hypotheses that propose medicinal benefits. However, in highly social capuchin monkeys, *Sapajus* and *Cebus* spp., anointing has been suggested to also benefit group members through 'social bonding'. To test this, we used social network analysis to measure changes in proximity patterns during and shortly after anointing compared to a baseline condition. We presented two capuchin groups with varying quantities of onion, which reliably induces anointing, to create 'rare resource' and 'abundant resource' conditions. We examined the immediate and overall effects of anointing behaviour on the monkeys' social networks, using patterns of proximity as a measure of social bonds. For one group, proximity increased significantly after anointing over baseline values for both rare and abundant resource conditions, but for the other group proximity only increased following the rare resource condition, suggesting a role in mediating social relationships. Social interactions were affected differently in the two groups, reflecting the complex nature of capuchin social organization. Although peripheral males anointed in proximity to other group members, the weak centrality only changed in one group following anointing bouts, indicating variable social responses to anointing. We suggest in part that anointing in capuchins is analogous to social grooming: both behaviours have an antiparasitic function and can be done individually or socially requiring contact between two or more individuals. We propose that they have evolved a social function within complex repertoires of social behaviours. Our alternative perspective avoids treating medicinal and social explanations as alternative hypotheses and, along with increasing support for the medical explanations for anointing, allows us to conceptualize social anointing in capuchins as 'social medication'.

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Anointing is a behaviour whereby animals acquire substances on their bodies by applying them directly, rubbing against a substrate or absorbing the chemicals from the environment (Messer & Bowler, 2018; Weldon, 2004). Such anointing often involves 'frenzied' rubbing of pungent materials into an animal's body or skin. A rich diversity of animals anoint, including fish, reptiles, birds and mammals (Clayton et al., 2010; de Roode et al., 2013; Brodie, 1977; Gasco et al., 2016; Hart et al., 1997; Huffman, 1997; Messer &

Bowler, 2018; Weldon, 2004). Although the anointing substrate varies by species and location (e.g. in captivity: Gasco et al., 2016; in free-ranging groups: Santos et al., 2019), anointing animals utilize plant-based materials, mud, peat, invertebrates and artificial substances found in their habitat (Alfaro et al., 2012; Baker, 1996; Zito et al., 2003).

There are three main functional hypotheses for why animals anoint. First, anointing may provide chemical defence against ectoparasites ('medicinal hypothesis': Clayton et al., 2010; Suárez-Rodríguez et al., 2013; Baker, 1996; Valderrama et al., 2000; Huffman, 1997; Alfaro et al., 2011; Meunier et al., 2008; Perry, 2008). Second, the behaviour may provide olfactory communication about

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status (chemosignalling or scent-marking hypothesis: [Paukner & Suomi, 2008](#); [Campbell, 2000](#); [Baker, 1996](#)). Third, it may reinforce or strengthen social bonds (social-bonding hypothesis: [Baker, 1996](#); [Leca et al., 2007](#); [Paukner & Suomi, 2008](#)). Each of these functional hypotheses has varying levels of support in studies of different species, suggesting some may be specific to certain species and/or anointing materials and moderated by access to resources and group mates ([Valderrama et al., 2000](#); [Paukner & Suomi, 2008](#); [Perry, 2008](#)). Also, the three functions are not mutually exclusive.

In primates, particular attention has been paid to anointing in social groups, leading to the definition of two modes of anointing; in ‘individual anointing’, an animal rubs substrate(s) onto the external surfaces of its own body, whereas in ‘social anointing’, an animal rubs its body or anointing materials against another individual during anointing ([Baker, 1996](#); [Alfaro et al., 2011](#); [Messer & Bowler, 2018](#)). Capuchin monkeys of the genera *Sapajus* (robust capuchins) and *Cebus* (gracile capuchins; see [Alfaro et al., 2012](#) for a taxonomic review) are ideal for studies of anointing. Both genera engage in social and individual anointing ([Alfaro et al., 2011](#)), and there is evidence for both chemical defence ([Baker, 1996](#); [Valderrama et al., 2000](#)) and social-bonding functions ([Leca et al., 2007](#); [Paukner & Suomi, 2008](#); see [Alfaro et al., 2011](#) for a review). Capuchins have a largely tolerant nature ([Fragaszy et al., 2004](#)), which is likely to be important in social anointing. Some comparisons of captive capuchin populations found that gracile capuchin monkeys, *Cebus capucinus*, anointed more socially than robust capuchin monkeys, *Sapajus apella*, which showed increases in aggression after anointing bouts ([Leca et al., 2007](#); [Paukner & Suomi, 2008](#)), but more recent reviews show that these genera or species level differences are minimal if present at all, with some groups of *Sapajus* spp. anointing at high frequencies and with low levels of aggression ([Alfaro et al., 2011](#); [Bowler et al., 2015](#); [Verderane et al., 2007](#)). One study found that wild wedge-capped capuchins, *Cebus olivaceus*, spent more time in proximity during anointing sessions than when not rubbing, leading the authors to suggest that anointing was reducing ‘competitive friction’ ([Valderrama et al., 2000](#)). Social anointing could therefore be increasing the cohesion of the whole group by strengthening the relationships between individuals. Alternatively, individuals may simply suppress aggression to access rare anointing materials in proximity to other monkeys. From the latter hypothesis, we might expect proximity values to rapidly return to baseline levels following bouts of anointing and to increase more when resources are rare and so monkeys must anoint socially to gain access to them.

Here, we aimed to test the social-bonding function of anointing by utilizing social network analysis to study capuchin monkeys’ social structure before and during and after anointing in two anointing conditions, in which we varied the density of available anointing materials and measured the monkeys’ proximity patterns. Using a different data collection methodology on the same anointing bouts, we have already shown that this group of capuchin monkeys all anointed socially, regardless of age–sex class, except for a recently introduced subadult male ([Bowler et al., 2015](#)). In this study, we focused on examining the monkeys’ proximity patterns across the conditions to explore any changes in the group social dynamics. As well as examining overall changes in social networks, since subadult males are typically peripheral to the group and therefore where changes in proximity might be most obvious, we sought to investigate the position and organization of peripheral males’ integration within the group social structure before, during and after anointing.

Social network analysis provides a tool to investigate the social structure of a group by monitoring individuals’ social relationships,

quantified through measuring the associations or interactions among individuals ([Whitehead, 2008](#); [Wey et al., 2008](#); [Voelkl and Kasper, 2009](#); [Krause et al., 2009](#); see [Sueur et al., 2011b](#) for a review). Within a social structure, individuals interact with others to form multiple relationships such that each relationship exists in a nexus of other relationships, which can mutually affect each other ([Hinde, 1983](#)). We measured social relationships in capuchins by monitoring proximity patterns, thus identifying association patterns to create a synthetic representation of the group social structure or network. By comparing the baseline (when anointing was absent) social structure of two groups of robust brown capuchin monkeys and simultaneously measuring proximity during- and after anointing in two types of anointing conditions, we aimed to detect any differences in group structure across the conditions.

The social-bonding hypothesis ([Baker, 1996](#); [Leca et al., 2007](#); [Paukner & Suomi, 2008](#)) proposes that animals strengthen social bonds by engaging in anointing behaviours in contact with group members. If, as suggested by this hypothesis, social anointing occurs to strengthen social bonds in a group, we predict that groups will be more tightly bonded (that is, we will observe an increase in individuals’ affinity for their group mates through increases in their proximity) immediately after anointing in comparison to baseline, regardless of the number of anointing resources provided.

Male–male capuchin bonds are weaker than female–female bonds; however, the extent of affiliation varies by species, location and the behaviour of the alpha male ([Fragaszy et al., 2004](#)). Subordinate male robust capuchin monkeys form smaller subgroups found on the periphery of the group’s territory ([Izawa, 1980](#)), likely due to the male emigration and female philopatry patterns documented in capuchin monkeys ([Fragaszy et al., 2004](#)). A similar pattern whereby lower-ranking males spend more time in the periphery of the group’s enclosures is observable in captivity ([Dufour et al., 2011](#)). This natural characteristic presents a unique opportunity to discover whether anointing socially reduces the competitive friction in a group of capuchins (as proposed by [Valderrama et al., 2000](#)) through changing peripheral males’ positions in their groups. The social-bonding hypothesis predicts that the peripheral males should be more integrated into their groups after anointing than before. Under the social-bonding hypothesis, we might also expect to see a change in the overall group networks following anointing.

METHODS

Study Site and Subjects

Subjects were 27 robust brown capuchins, *S. apella*, housed in two separate groups, in the ‘Living Links to Human Evolution’ Research Centre (hereafter Living Links) in Edinburgh Zoo; the East group ($N = 13$), and the West group ($N = 15$). The two groups were kept in separate enclosures with access to their own indoor (7×4.5 m and 6 m high) and outdoor (approximately 900 m²) areas ([Leonardi et al., 2010](#) and [Macdonald & Whiten, 2011](#), provide further details about Living Links and associated animal husbandry).

Although both groups contained a mixture of males and females, adults, subadults, juveniles and infants, the group compositions were markedly different ([Table 1](#)). The West group consisted of one main female matriline of 13 related individuals with two further unrelated males, the alpha male (Diablo) and another adult male (Diego). However, the East group contained two main female matriline of four and seven related individuals with two unrelated males, the alpha male (Popeye) and another adult male (Kato). All individuals except Diablo and Kato were born in captivity. As beta males have been observed with other males in peripheral male groups in wild observations (e.g. [Izawa, 1980](#)), we included all the

Table 1
Monkey group compositions

Age–sex classification		East group	West group
Adults	Male	4 (Popeye, Manuel, Kato, & Carlos)	4 (Diablo, Diego, Toka, & Figo)
	Female	3 (Anita, Junon, & Penelope)	3 (Lana, Santi, & Sylvie)
Subadults	Male	1 (Chico)	1 (Micoe)
	Female	0	1 (Pedra)
Juveniles	Male	1 (Reuben)	3 (Inti, Rufou, Ximo)
	Female	2 (Rosa & Sol)	0
Infants		2	2 (1)

We define age–sex classifications according to Izawa, 1980. One infant (shown in parentheses) was born during the study (monkey names included in the social network analysis are shown in parentheses).

subordinate adult males in our peripheral male analysis (three from the East and three from the West group).

We used white onions, *Allium cepa* (diameter >7 cm) to elicit anointing behaviours. Onions have been used successfully to elicit rubbing in other studies of anointing in capuchin monkeys (see Alfaro et al., 2011 for a review), and are known to produce antibacterial, antidermatophytic and antioxygenic substances (Meunier et al., 2008). All outer layers were left intact, and each onion was sliced in half immediately before being introduced to the monkey's outdoor enclosure. If a capuchin monkey in our research groups is supplied with an onion, it will reliably bite into it and vigorously rub the exudates over its body, often also anointing socially with group mates (Bowler et al., 2015). As capuchin monkeys are known to anoint with other pungent materials, before the study, we removed onions and leeks along with other strong-smelling materials (such as herbs, garlic and limes) from the monkeys' regular diet to reduce any other potential opportunities for anointing outside of the observation sessions. We replaced these items with alternative food and enrichment sources.

Experimental Conditions

To determine any changes in the monkeys' social dynamics, we measured proximity between dyads over five different conditions: (1) baseline; (2) during anointing, rare resources; (3) after anointing, rare resources; (4) during anointing, abundant resources; and (5) after anointing, abundant resources.

In the 'rare resource' condition, we introduced half an onion into the monkey's enclosure for the whole group, and in the 'abundant resource' condition, we introduced half an onion to the enclosure per independently mobile individual. We presented the monkeys with anointing materials twice a week, with rare and abundant resource conditions counterbalanced across days. We randomly determined in advance of the study whether onions would be presented to the East or West group first. In a separate baseline condition, data were collected over the same time frame using the same proximity measure but not on the same days as the anointing sessions, so no onions or other anointing materials were available.

During the two types of anointing conditions and baseline condition, monkeys had access to their indoor and outdoor enclosures and an off-show area not visible from the observation area.

Proximity Measures

We examined the monkeys' proximity patterns using scan sampling (Altmann, 1974) at 4 min intervals. Thus, we classified dyads as 'within 40 cm of each other' as being within close proximity and any dyads 'more than 40 cm' as being apart. For monkeys in close proximity, we did not differentiate between those in contact or not.

Procedure

At the beginning of each anointing session, before we introduced the onions to each group, an initial 'start scan' was recorded, noting the location and the proximity of each monkey, confirming they were all visible. From an elevated platform we then threw onions into a defined area in the monkeys' outside enclosure (approximately 5 × 5 m). Scan sampling commenced 1 min after we observed the first instance of anointing. Anointing behaviours were defined as a monkey actively rubbing an onion onto the external surfaces of its body, rubbing its body against another monkey's body or another monkey's held onion. Each scan took up to approximately 3 min for all the monkeys to be accounted for or marked as out of sight. We repeated subsequent scans every 4 min until 45 min had elapsed, or 10 min after the last monkey ceased anointing, whichever was later. We recorded any monkey(s) out of sight during the 4 min scan as such, and subsequently removed them from the analysis.

We collected scan data in 26 sessions, each of 45 min, for both the West group (13 sessions in the rare resource condition and 13 in the abundant resource condition) and the East group (12 sessions in the rare resource condition and 14 sessions in the abundant resource condition). Two further sessions were collected but removed from the analysis due to experimenter error during data collection (one from the West and one from the East group). We included all infants in the scan sampling for the five conditions, but four (two from the East and two from the West group) were subsequently removed from the data set because they were not independent of their mothers during the data collection (all being 2 months old or less at the start of the study).

Data Analysis

We separated anointing session scan data into during and after anointing conditions. Thus, during anointing includes all scans until the last incidence of anointing by all the monkeys in each session, whereas after anointing includes all the scans after the last incidence of anointing until the end of the anointing session. All independently mobile monkeys engaged in anointing during the study but the amount of time spent anointing varied by session, group and the two types of anointing conditions. Thus, the number of scans that make up our anointing conditions varies by group and condition (Table 2). A detailed analysis of the proportions of social and individual anointing by each monkey in the two groups using focal animal sampling, collected independently during the same anointing bouts, has already been published (Bowler et al., 2015).

Association indices were built based on the proximity patterns between dyads in the five conditions using the simple index ratio (Hinde, 1976). This index considers the number of instances in which two individuals are observed interacting (or

Table 2
Scan sample sizes across the five conditions for the East and West groups

Condition	East group	West group
During anointing, rare resources	52	50
After anointing, rare resources	92	106
During anointing, abundant resources	103	76
After anointing, abundant resources	72	82
Baseline	99	99

The West group experienced 13 sessions in the rare resource condition and 13 sessions for the abundant resource condition, while the East group experienced 12 sessions in the rare resource condition and 14 sessions for the abundant resource condition.

in our case in proximity) divided by the number of instances in which at least one of these individuals is present (see Whitehead, 2008; Whitehead, 2009b; Whitehead, 2009a for more information on the simple index ratio and other available indices). A score closer to one indicates that a pair of individuals was often together and thus the two were more tightly associated. A score closer to zero shows the individuals were more often apart. We combined the association indices to form a matrix of indices for each group and each condition. To produce the corresponding sociograms, we filtered all the association indices through the same pipeline in the visualization program Gephi 0.9.2 (Bastia, Heymann, & Jacomy, 2009).

'Strength' was selected as the ideal network statistic measure to represent each individual's 'connectedness' within the overall group social structure of monkeys for the first two sets of analyses. Strength is the sum of the association indices between an individual and its neighbours. As a result, strength is high when an individual has many associations with other individuals in the network or has strong associations with others (i.e. when the focal individual is close to others) or both (Whitehead, 2009b). Finally, in our second analysis, we used eigenvector centrality measures to examine any changes in the peripheral males' positions in their groups after anointing, indicating a potential change in their group integration. Eigenvector centrality is a network statistic that measures how strongly an individual is associated with other individuals and how strongly those other individuals are themselves associated (Whitehead, 2008), making it an ideal measure to assess peripheral male integration within the group.

We used two-tailed Friedman's tests and Wilcoxon signed-rank tests in R (R Core Team, 2019) to examine any changes in each group's social structure by examining strength scores between the five conditions with α set as 0.05. We used SocProg 2.4 (Whitehead, 2009b) to generate network statistics based on the associations of each monkey within its group in each of the five conditions. To address any changes in group integration resulting from anointing, we examined the peripheral males' centrality during anointing and immediately after anointing in the two resource conditions with the baseline condition.

Ethical Note

This study was approved by the University of St Andrews School of Psychology and Neuroscience Ethics Committee under the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching. The Living Links Centre Research Team of the University of St Andrews and the Royal Zoological Society of Scotland (RZSS), Edinburgh Zoo also approved the study. Monkeys received their typical daily diets, and water was available ad libitum throughout the observations.

RESULTS

Group Social Networks

We constructed five social networks (hereafter 'sociograms') for each group based on the capuchin monkeys' association indices during each of the five conditions (Figs. 1 and 2). This allowed us to compare the monkeys' social structure in the baseline (no onions present), with their compositions during and after anointing in the two resource conditions (rare and abundant resources).

Comparing Group Network Structures

Comparisons between group social dynamics across the five conditions

Increased association during anointing could be the result of monkeys engaging in anointing activities. However, if the social-bonding hypothesis is correct, we would expect to see an increase in strength immediately after anointing is over. To explore whether anointing influenced the proximity patterns of the groups in this manner, we compared measures of strength across the five conditions. We found a significant difference between them (Friedman: $\chi^2_4 = 22.7$, $P < 0.001$) with a relatively low effect size (Kendall's $W = 0.237$).

Owing to differences in the number of matrilineal lines in the groups, we compared strength scores between the baseline and during and after anointing in the two resource conditions (rare and abundant resources) followed by Wilcoxon signed-rank tests for each group separately. In the East group, strength scores were higher after anointing in the rare resource condition compared to the baseline ($Z = 61$, $P = 0.01$; Fig. 3) and higher after anointing in the rare resource condition than after anointing in the abundant resource condition ($Z = 7$, $P = 0.019$; Fig. 3). We found no other significant effects.

In the West group, strength was higher in all experimental conditions compared with those in the baseline. It was higher in both abundant resource conditions compared to both rare resource conditions, and higher during than after anointing in the abundant resource condition. When resources were abundant, strength was higher both during and after anointing than during the baseline (during anointing and baseline: $Z = 0$, $P < 0.001$; after anointing and baseline: $Z = 86$, $P = 0.002$; Fig. 4). When the West group had rare resources, strength was also higher both during and after anointing compared to the baseline condition (during anointing and baseline: $Z = 0$, $P = 0.002$; after anointing and baseline: $Z = 80$, $P = 0.013$; Fig. 4). Their strength scores were also higher during than after anointing in both the rare ($Z = 13$, $P = 0.021$; Fig. 4) and the abundant resource condition ($Z = 2$, $P = 0.003$; Fig. 4). Across the resource conditions, strength scores were also higher after anointing in the abundant resource condition than after anointing in the rare resource condition ($Z = 80$, $P = 0.013$; Fig. 4). We also found higher strength scores during anointing in the abundant resource condition than during anointing in the rare resource condition ($Z = 85$, $P = 0.003$; Fig. 4). Finally, strength scores were higher during anointing in the abundant resource condition than they were after anointing in the rare resource condition ($Z = 0$, $P < 0.001$; Fig. 4), although there were no differences between strength scores after anointing in the abundant resource condition and scores during anointing in the rare resource condition. These results suggest that the East and West groups' social structures were impacted differently by anointing and resource density.

Individual monkeys' strength scores differed across the five conditions (Table A1) and between the groups. Median strength scores were lower for the East than the West group (Figs. 3 and 4).

Notably, several individuals had low baseline measures of strength compared to the rest of their group members (East group: $N = 4$: Kato, Carlos, Junon and Manuel; West group: $N = 2$: Toka and Pedra; Table A1). Kato, Carlos, Manuel and Toka were all subordinate adult males, Junon was an adult female (the lower ranking female matriarch of the East group's second matriline) and Pedra was a subadult female, the only subadult female in either group. All these low baseline measures of strength indicate that these individuals had fewer associations with other members of their respective groups.

Peripheral Male Network Position

There were six peripheral males in Living Links (three in the East and three in the West groups, indicated by the uppercase names in the sociograms in Figs. 1 and 2). To address any changes in these individuals' group integration, for each group separately, we compared their eigenvector centrality measures, both during and after anointing in the two resource conditions (rare and abundant), with the baseline. Only the West group peripheral males' eigenvector centrality measures differed between the baseline and during and after anointing in the two resource conditions (Freidman test: $\chi^2_4 = 10.9$, $P = 0.028$; Fig. A1), with a large effect size (Kendall's $W = 0.905$). We found no differences in the East group (Freidman test: $\chi^2_4 = 8.55$, $P = 0.073$), but a large effect size (Kendall's $W = 0.713$). Thus, although these males were all engaging in anointing (including social anointing, E. Messer & M. Bowler, personal observation), we found an effect on their centrality only in the West group. Follow up Wilcoxon tests revealed no differences

between the combinations of the five conditions for the three peripheral males from the West group.

To better understand the effect of anointing on the rest of the groups' members, we examined their centrality scores across the five conditions. We found no difference in the connectedness of the remaining group members for the East or West group between the baseline and during and after anointing in the two resource conditions (Freidman test: East group: $\chi^2_4 = 1.92$, $P = 0.750$; West group: $\chi^2_4 = 4.06$, $P = 0.398$) with a relatively low effect size (Kendall's $W = 0.0765$). This indicates that anointing, regardless of resource abundance, did not affect the remaining monkeys' centrality scores.

DISCUSSION

We observed that capuchin monkeys enthusiastically anointed whether resource density was high or low. However, the effect of anointing on their social dynamics varied by group and the density of resources available. While we found increased levels of association after anointing for the West group regardless of resource density, the East group monkeys increased their associations after anointing only when the resource was rare.

When resources were sufficiently plentiful for every monkey to have a piece of onion, strength values in the West group were significantly higher (either having stronger or more associations with others) after anointing in both resource conditions compared to the baseline. This suggests that anointing can mediate social relationships, since monkeys did not need to increase proximity to

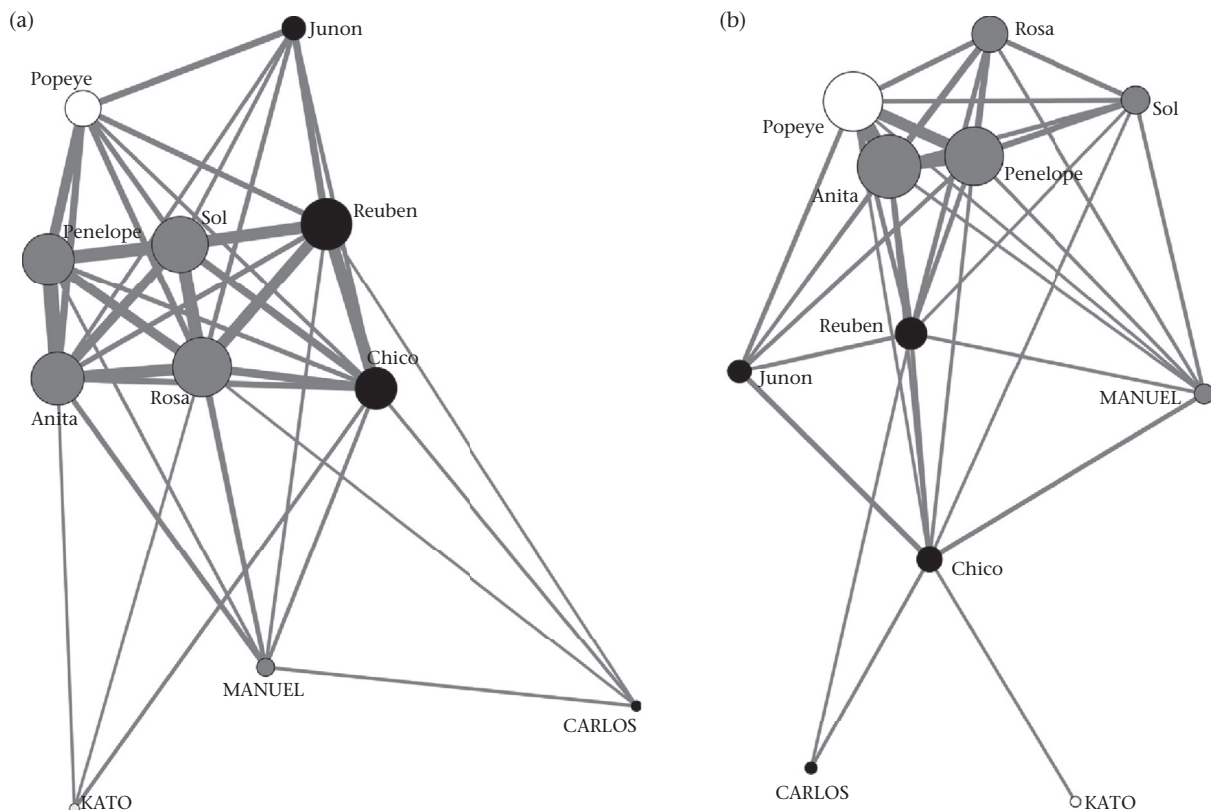


Figure 1. Sociograms for the East group. The group social structure is shown (a) in the baseline condition, (b) during anointing in the rare resource condition, (c) after anointing in the rare resource condition, (d) during anointing in the abundant resource condition and (e) after anointing in the abundant resource condition. Nodes represent each monkey, with the peripheral males indicated by uppercase letters. The size of these nodes is proportional to strength, calculated for each monkey (also see Table A1 for these scores), and the edges joining the nodes are proportional to bond strength. There are two separate matrilineal indicated by black and dark grey nodes. Unrelated individuals' nodes are white.

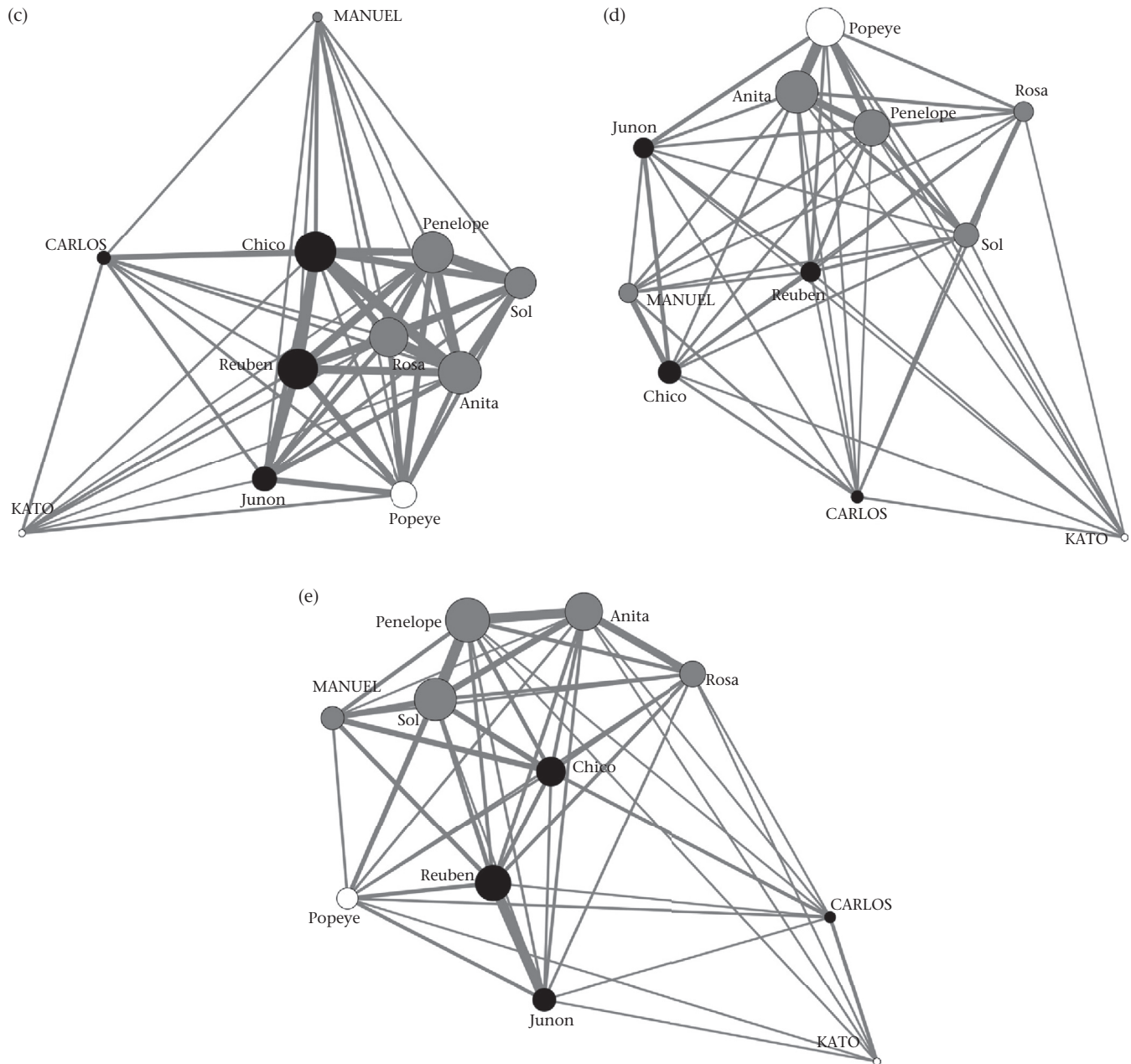


Figure 1. (continued).

anoint in the abundant resource condition. Moreover, their associations were highest after anointing in the abundant resource condition compared to the rare resource condition, showing that the monkeys chose to continue to associate together after anointing. Conversely in the East group, we found that the monkeys' associations were highest after anointing in the rare resource condition, indicating that the monkeys remained closer together than in the baseline condition after anointing only when they would have had to come close together to gain access to limited materials. Thus, associations with group members were higher after anointing regardless of the density of available resources for the West monkeys. By contrast in the East group, we saw changes in social structure emerge after anointing when resource density was lower, an increase in proximity patterns that could in part be due to the limited resources available.

During anointing, the West group's associations increased above the baseline in the two anointing conditions, but the effect was greater in the abundant resource condition. Thus, when resource density was higher, which could facilitate individual anointing and decrease associations, monkeys in the West group were opting to increase their associations. Conversely, in the East group, we found no differences in the monkeys' associations during anointing in either of the two resource conditions compared to the baseline. Therefore, although the East group engaged in anointing, the effect on their social structure was only evident after anointing, perhaps after the monkeys had to come together to access the limited resource. These group differences are likely to be a reflection of the complex nature of capuchin social organization.

Differing social dynamics within the East and West groups could be contributing to these differing results. The West group was

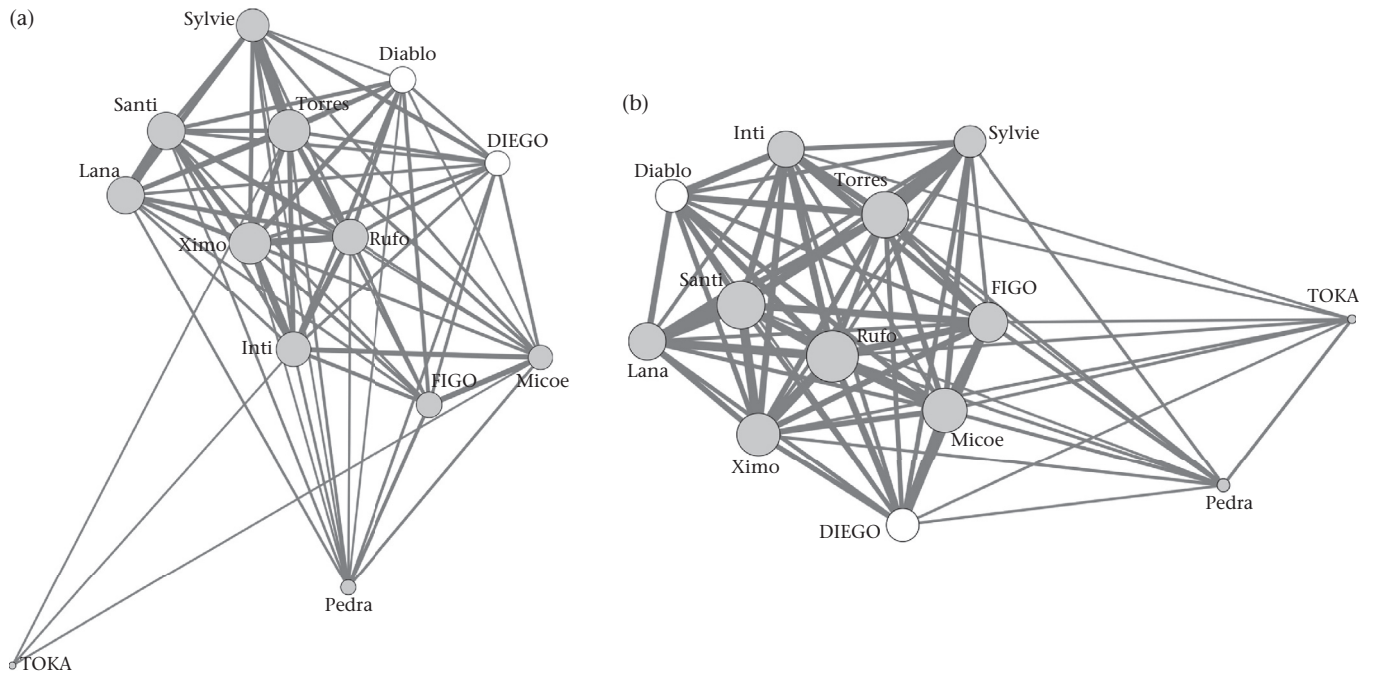


Figure 2. Sociograms for the West group. The group social structure is shown (a) in the baseline condition, (b) during anointing in the rare resource condition, (c) after anointing in the rare resource condition, (d) during anointing in the abundant resource condition and (e) after anointing in the abundant resource condition. Nodes represent each monkey, with the peripheral males indicated by uppercase letters. The size of these nodes is proportional to strength, calculated for each monkey (also see Table A1 for these scores), and the edges joining the nodes are proportional to bond strength. There is a single matriline represented by light grey nodes. Unrelated individuals' nodes are white.

formed of one main matriline plus two unrelated adult males, whereas the East group had two main matriline and two unrelated adult males. Thus, from the outset, the West group individuals had a higher level of overall relatedness between individuals than the East group. Indeed, Welker, Hoehmann and Schaefer-Witt (1990) have argued that the matriline in their captive *Cebus apella* formed the foundation of the group's social structure (Fragaszy et al., 2004). As such, the West group's main single matriline versus the East group's two matriline could be contributing to the changes in social dynamics we report. Future work examining the function of social bonding in other capuchin monkeys' anointing behaviour should seek to include measures of relatedness between individuals.

In capuchins, the matriline underlie rank structures that affect access to resources and social organization. In our two groups of capuchins, the more dominant group members could monopolize resources from subordinates which tended to wait. All the monkeys with the lowest baseline measures of strength (four males: Kato, Toka, Carlos and Manuel; two females: Junon and Pedra) were subordinates. Junon was the only adult female to have a baseline strength score less than one, likely because she was from a different matriline, and subordinate to the two other adult females. While we may expect the four subordinate males to have had lower baseline strength, perhaps indicating they were the most likely to be peripheral males, Pedra's (our only subadult female) low strength was less expected and may change as she reaches sexual maturity.

Our social network analysis provides some support for the social-bonding hypothesis (see also Leca et al., 2007; Paukner & Suomi, 2008; Valderrama et al., 2000), particularly in the West group, where there was an increase in group cohesion in the short term after anointing. Analysis of longer-term changes in social dynamics over time following differing access to anointing

materials would provide further insight into any longer-term changes to group social structure.

Only the West group peripheral males' overall integration (connectedness) into their group differed across the five conditions, as peripheral males increased associations during anointing. Although all the peripheral males were engaging in social anointing (E. Messer & M. Bowler, personal observation), and potentially gaining from the functional benefits of reaching inaccessible and nonvisible areas of their body (as we have previously shown with the same group of capuchin monkeys, Bowler et al., 2015), changes in their social integration were not detectable in the East group. This difference might be due to individual differences between the males' positions in the dominance hierarchy of their respective groups. Although both groups had subordinate males with low baseline associations (e.g. Kato and Carlos in the East group and Toka in the West group), both groups also contained subordinate males that had higher centrality scores (e.g. Manuel in the East group, and Diego and Figo in the West group). Moreover, in the West group, Diego, a beta male, became the alpha male after the study. Future work excluding beta males in peripheral male subgroups (e.g. Izawa, 1980) and including more data collected on the social network position of other peripheral males to increase the sample size would be useful to examine any subtler changes, for example in competitive friction. When we compared the rest of the group centrality measures without the peripheral males', we found no significant effect of anointing, indicating that the remaining monkeys did not become more integrated into the groups after anointing. Thus, although anointing impacted the monkeys' strength scores, these associations may be short lived. We surmise that anointing with onions in robust capuchin monkeys appears to impact individual connectedness rather than group integration.

Because we focused on monkey proximity patterns and collected scan data every 4 min, we could not accurately assess who

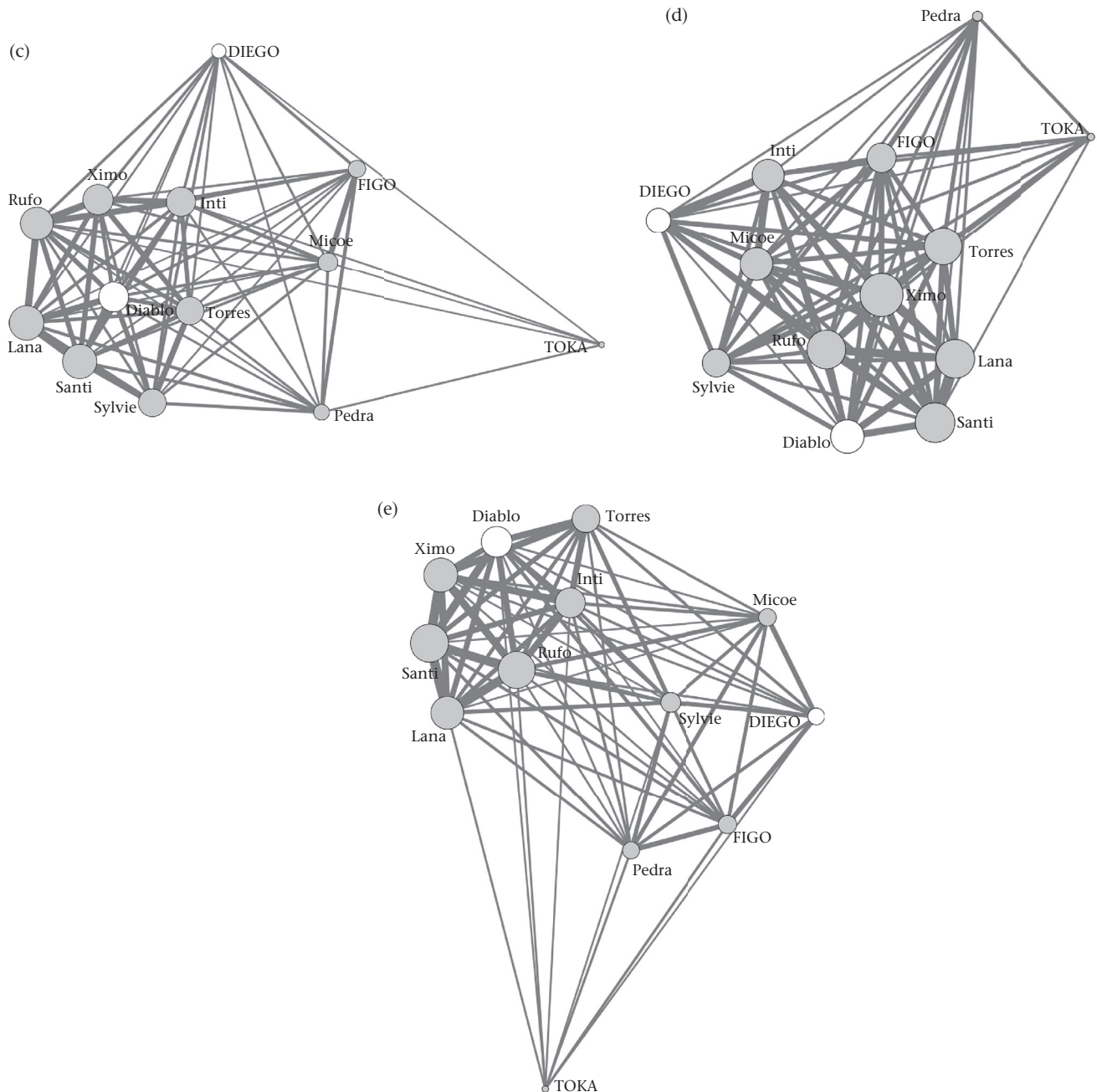


Figure 2. (continued).

joined whom and how monkeys reacted to these aggregations during anointing. To provide further insights into the impact of such social influences and the effect of resource density on individuals' proximal choices, future work could explore the spread of social and individual anointing over time in groups of monkeys, and any contagious effects of the behaviour.

In capuchins, anointing has an apparent role in self-medication (Alfaro et al., 2011). Previous studies of anointing have shown that social anointing may be an entirely functional extension of this, helping to provide medicinal coverage for group members (e.g. Bowler et al., 2015), which may be relatives or potential hosts for infectious parasites. As such, these phenomena may also provide some insight into the basis of human healthcare networks where individuals care for the sick (Kessler, 2020). Future work examining any changes in group structure during social

anointing could provide further insights into anointing as social medicine.

Here we have shown that anointing in robust capuchin monkeys affected social behaviour through increased and/or stronger associations. There is perhaps a strong partial analogy here with grooming, shown in capuchin monkeys to serve various hygiene and social functions (Fragaszy et al., 2004). Autogrooming appears to fill an obvious role of removing ectoparasites and other debris while social grooming (allogrooming) extends this benefit by reaching parts of the body that an individual cannot reach itself by a groomer actively grooming another individual (Barton, 1985). Adding to this, groomers could also benefit if they consume parasites they remove. However, there is also plentiful evidence that social grooming serves additional social functions (di Bitetti, 1997; Dunbar, 1991; Sánchez-Villagra et al., 1998;

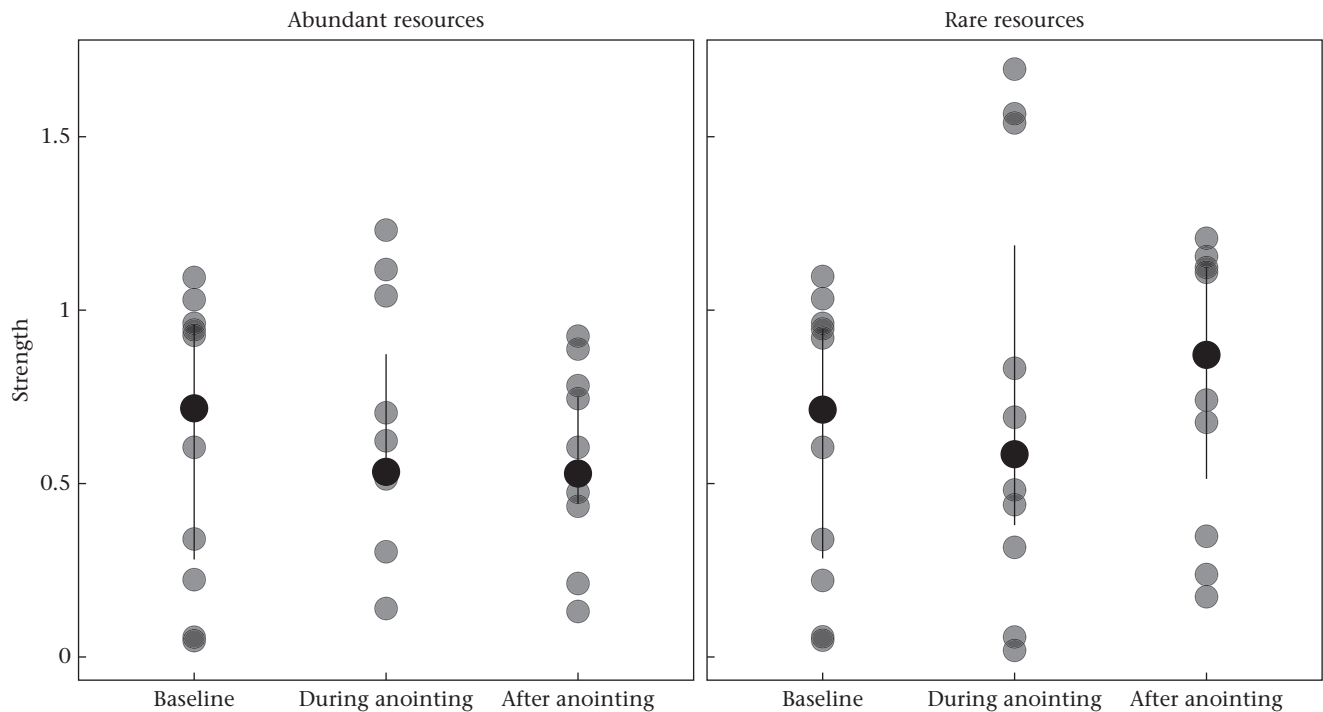


Figure 3. Median measures of strength in the East group during and after anointing in the two resource conditions (abundant and rare) and baseline condition. Error bars represent the interquartile range and greyed circles the data points.

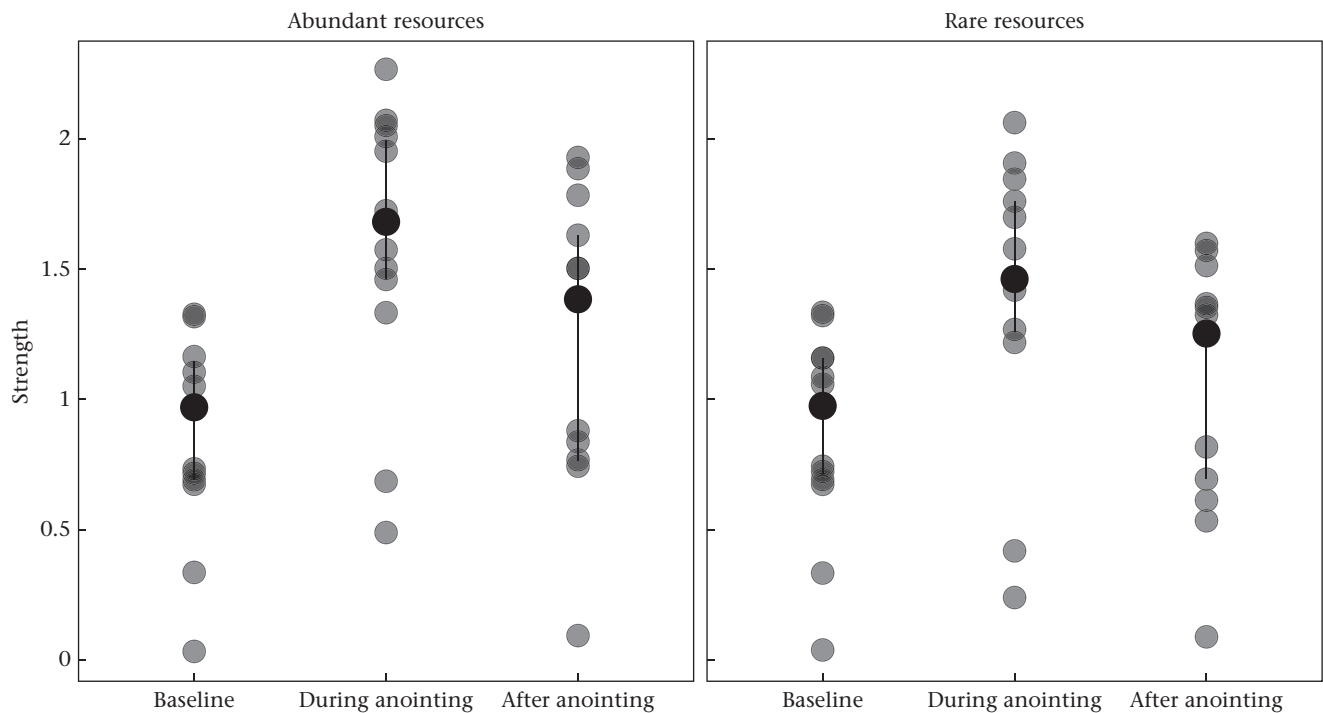


Figure 4. Median measures of strength in the West group during and after anointing in the two resource conditions (abundant and rare) and baseline condition. Error bars represent the interquartile range and greyed circles the data points.

Nunn, Altizer, & Altizer, 2006), with individuals prioritizing grooming with those ranked slightly higher than themselves (Seyfarth, 1977; but see Parr et al., 1997 which indicates that robust capuchins are more likely to groom other closely ranked individuals). Although grooming likely changes with the social

organization and varies with ecological conditions (e.g. see Lazaro-Perea, de Fátima Arruda, & Snowdon, 2004), it has also been shown to be a resource to be traded with others such as for food sharing (de Waal, 1997; but this can be affected by rank differences, e.g. see Jaeggi et al., 2013), or support in aggressive

disputes (Hemelrijk, 1994; Seyfarth, 1977; Seyfarth & Cheney, 1984).

Conclusion

Social and medicinal hypotheses for anointing are not mutually exclusive, and while the widespread nature of anointing within the primates and other taxa suggests that there is an underlying nonsocial benefit to the behaviour, like grooming, anointing in capuchin monkeys has evolved within the context of a highly complex repertoire of social behaviours and may have taken on an additional social function. The complexity of social behaviour in these monkeys may make separating the cause and effect of anointing on social structure challenging. Our alternative perspective departs from treating medicinal and social explanations as alternative hypotheses, and along with increasing support for the medical explanations for anointing, justifies describing anointing in capuchin monkeys as 'social medication'.

Author Contributions

All authors contributed to the study conception and design. E.J.E.M. and M.T.B. performed the data collection. E.J.E.M. and N.C. performed the data analysis. E.J.E.M. wrote the manuscript and all authors provided editorial advice and approved the final manuscript.

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Appendix

Table A1

Strength scores for monkeys in the baseline and two resource conditions

Group	Monkey	Age–sex classification	Baseline	Rare resources		Abundant resources	
				During anointing	After anointing	During anointing	After anointing
East group (N=11)	Anita	Adult female	0.96	1.69	1.23	1.2	0.78
	Carlos	Subordinate adult male	0.06	0.06	0.3	0.35	0.21
	Chico	Subadult male	0.72	0.48	0.62	1.15	0.6
	Junon	Adult female	0.34	0.44	0.54	0.67	0.47
	Kato	Subordinate adult male	0.05	0.02	0.14	0.17	0.13
	Manuel	Subordinate adult male	0.22	0.31	0.51	0.24	0.47
	Penelope	Adult female	0.94	1.54	1.04	1.15	0.92
	Popeye	Dominant adult male (alpha)	0.6	1.56	1.11	0.74	0.43
	Reuben	Juvenile male	0.92	0.69	0.53	1.12	0.74
	Rosa	Juvenile female	1.09	0.83	0.53	1.1	0.53
	Sol	Juvenile female	1.03	0.58	0.7	0.87	0.88
West group (N=13)	Diablo	Dominant adult male (alpha)	0.74	1.26	1.68	1.35	1.5
	Diego	Subordinate adult male	0.69	1.26	1.33	0.53	0.74
	Figo	Subordinate adult male	0.72	1.58	1.5	0.69	0.74
	Inti	Juvenile male	1.05	1.42	1.57	1.32	1.51
	Lana	Adult female	1.15	1.46	1.95	1.6	1.62
	Micoe	Subadult male	0.67	1.76	1.72	0.81	0.84
	Pedra	Subadult female	0.33	0.42	0.68	0.61	0.77
	Rufo	Juvenile male	1.09	2.06	2.07	1.5	1.89
	Santi	Adult female	1.16	1.9	2.05	1.58	1.93
	Sylvie	Adult female	0.98	1.22	1.46	1.24	0.87
	Toka	Subordinate adult male	0.03	0.24	0.49	0.08	0.09
	Torres	Infant	1.32	1.84	2	1.25	1.38
	Ximo	Juvenile male	1.31	1.7	2.26	1.37	1.78

Scores from the rare and abundant resource conditions are based on the monkeys' proximity patterns across all the 45 min anointing sessions for each group. These scores are proportional to the size of the nodes in Figs. 1 and 2.

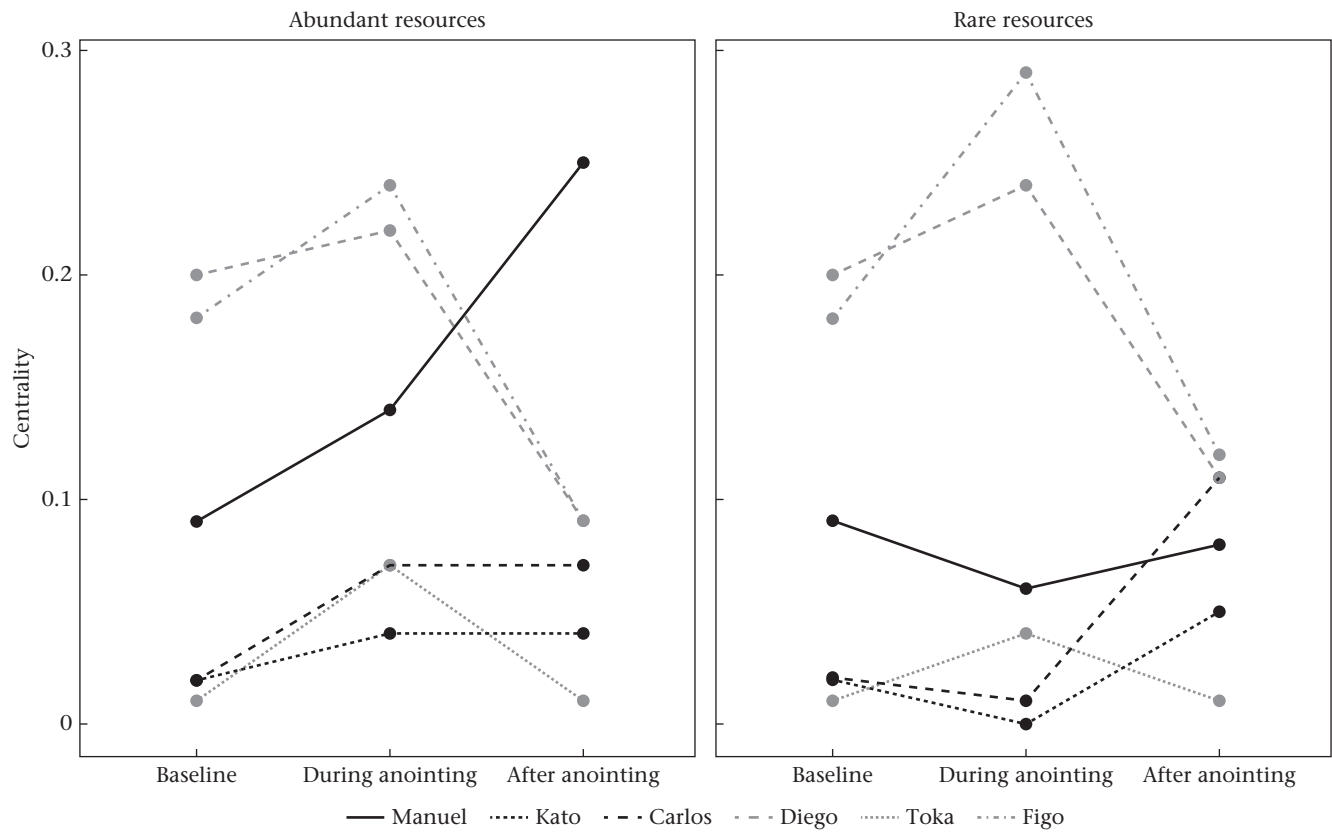


Figure A1. Centrality scores for each peripheral male in the East (black) and West (grey) groups during and after anointing for the abundant and rare resource conditions compared with the baseline.