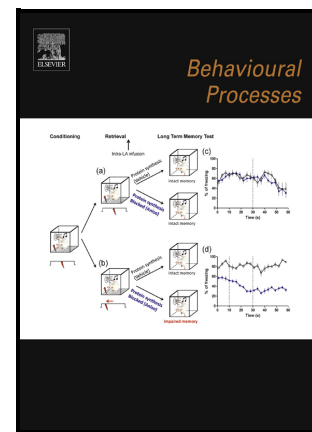


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## The effects of allogrooming and social network position on behavioural indicators of stress in female lion-tailed macaques (*Macaca silenus*)

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### Abstract

Allogrooming serves an important social function in primates and confers short term benefits such as parasite removal and stress-relief. There is currently mixed evidence as to the immediate impact of allogrooming on an individual's stress levels, which may be influenced by their role in the grooming dyad, position in their social network, or their relationship with their grooming partner. In this study of seven captive adult female lion-tailed macaques (*Macaca silenus*) in a mixed sex group at Chester Zoo, UK, we found evidence to support a tension-reduction function of allogrooming. Focal animal sampling showed that the duration of self-directed behaviour (SDB), which indicates moderate to high levels of stress, was significantly lower in the five-minute period following allogrooming than the five-minute period preceding it for both recipients and groomers. However, when compared to match-control periods, both SDB rates and durations were significantly lower across all individuals in the five-minute period both before

and after allogrooming, indicating that although allogrooming reduces stress, it is also more likely to occur when individuals are already in a relatively relaxed state. The rate and duration of SDB post-grooming did not correlate with the strength of a dyad's bond (based on proximity). This suggests that it is the act of allogrooming itself, rather than the identity of the partner, that reduces stress for both parties. Analysis of the proximity network highlighted a clear cost to social integration; node strength, a measure of the number and strength of an individual's direct relationships, positively correlated with the duration of self-directed behaviour, suggesting that more gregarious individuals may experience higher levels of stress. These findings add to the growing body of literature that examines the effect of the individual social environment on primate stress levels, and also highlight the need to further investigate the link between social integration and the stress experienced by group-living animals.

### Key Words

Allogrooming; Indirect connections; Stress; Social network analysis; Welfare

### 1. Introduction

Allogrooming helps to establish, maintain and repair social relationships in primates (Dunbar, 1991, Lehmann et al., 2007). Because high quality social bonds correlate with increased infant survival (Silk et al., 2003, 2009) and longevity (Archie et al., 2014, Campos et al., 2020), this function is extremely important. Allogrooming is also shown to have short-term benefits for individuals including a tension-reduction function (Terry 1970, reviewed in Russell & Phelps 2013). Primates increase allogrooming following a stressful event (eg. vervet monkeys (*C. aethiops*, Cheney, 1992); Hamadryas baboons (*Papio hamadryas hamadryas*, Judge et al., 2006); samango monkeys (*C. m. erythrarchus*, Payne et al., 2003), and a short-term post-

grooming reduction in stress in allogrooming recipients, has been inferred from a reduction in heart rate (Aureli et al., 1999), a release of opioids in the blood (Martel et al., 1995), or a lower frequency of stress-related, self-directed behaviours (SDB, Radford, 2012).

The importance of allogrooming in tension reduction for groomers is less clear. Rates of SDB in captive female crested black macaques (*Macaca nigra*) were lower after grooming others than in comparable time periods (Aureli & Yates, 2010), and in female Barbary macaques (*Macaca sylvanus*), the concentration of faecal glucocorticoid (FGC) metabolites is negatively correlated with the amount of grooming given (Shutt et al., 2007). However, in both cases more relaxed individuals may simply be more likely to partake in grooming of others (Semple et al., 2013).

An individual's social environment can also influence both their chronic and acute stress levels. Across primate taxa, subordinate individuals have higher relative cortisol levels when subjected to a high rate of stressful events, than more dominant individuals (Abbott et al., 2003), and socially isolated male yellow baboons (*Papio cynocephalus*) have higher basal cortisol concentrations than more socially affiliated males (Sapolsky et al., 1997). Social network analysis has also revealed a link between an individual's place in the social network and physiological measures of stress. For example, high-ranking pregnant female rhesus macaques' (*Macaca mulatta*) faecal glucocorticoid levels decrease with reach (the number of connections an individual has with others in the group of two or fewer paths in length), suggesting that individuals within more tight-knit proximity networks are less stressed (Brent et al., 2011). The opposite was found in a group of male and female humans, with salivary cortisol levels inversely correlated with the number of outgoing ties (Kornienko et al., 2014). Olive baboons (*Papio hamadryas anubis*) occupying central physical positions in the group have higher faecal glucocorticoid (FCG) concentrations than those on the edge (Tkaczynski et al., 2014), and rhesus macaques exhibit more frequent SDB (scratching) around individuals with whom they are less bonded (Whitehouse et al., 2017). The relationship between stress levels, social environment, and the effectiveness of allogrooming appears to be complex.

Self-directed behaviours (SDB) are a reliable behavioural indicator of chronic stress in primates. These behaviours are often apparently irrelevant to the situation in which they occur, such as scratching, self-grooming, yawning, and shaking (Maestriperi et al., 1992) and reliably indicate both psychological and physical stress (Maestriperi et al., 1992, Troisi, 2002). They increase in frequency following stressful events, such as conflict situations (Koski et al., 2007, Schino et al., 2007, Daniel et al., 2008); perceived threats (Gustison et al., 2012), and in female baboons following the birth of an infant (Brent et al., 2002). Anxiety-inhibiting drugs decrease the frequency of SDB in male long-tailed macaques (*Macaca fascicularis*), with the converse true for anxiety-increasing drugs (Schino et al., 1996).

Relatively little is known regarding the relationship between allogrooming and SDB. Allogrooming is associated with a decreased rate of SDB in laboratory crab-eating macaques (*Macaca fascicularis*, Lee et al., 2012). In contrast, wild Barbary macaques increase time self-grooming after allogrooming sessions, whether the groomer or groomee (Molesti & Majolo, 2013). In this study, we measured rate and duration of SDB in a group of captive lion-tailed macaques (*Macaca silenus*) as an indicator of stress to test three main questions. Firstly, whether participation in allogrooming leads to a reduction in the rate and duration of SDB, and whether the effect is stronger for the recipient than the groomer. Secondly, whether a stronger social bond within an allogrooming dyad is associated with a greater reduction in reduced stress post allogrooming. Finally, individual social network position is associated with baseline stress levels, as measured by the likelihood to show SDBs.

## **2. Material and Methods**

### **2.1 Ethical note**

This study was approved by Manchester Metropolitan University's Science and Engineering Research Ethics and Governance Committee Ref:33782.

## **2.2 Subjects and study site**

Study subjects were seven adult females aged 11–21 years, living as part of a group of lion-tailed macaques (*Macaca silenus*) at The North of England Zoological Society (Chester Zoo), Chester, UK. At the time of study, the group comprised of three adult males, seven adult females, two sub-adult females (aged six years but not yet given birth) and four juveniles (from one to five years). All the adult females included in data collection were closely related (parent, offspring, sibling or half sibling) to between three and six other adult females in the group. All juveniles were weaned, mothers were not lactating, and no females were visibly pregnant.

The macaques were housed in a large indoor enclosure (1092m<sup>3</sup>) connected by three tunnels to an outdoor area (793m<sup>2</sup>). Access to the landscaped outdoor area containing trees, poles, ropes and surrounded by a water moat, was available at all times with the exception of any necessary cleaning and maintenance work. The macaques were scatter fed at various times throughout the day, with additional food-based enrichment provided *ad hoc*. Drinking water was available at all times.

## **2.3 Data collection**

All behavioural data were collected over 16 days between 30/07/14 and 28/08/14 and 10 days between 14/09/14 and 31/10/14, by KY, from 10:00 to 16:30, excluding times during

which the macaques were fed. To ensure results were not influenced by gender or age class of grooming partner, we focussed only on adult females.

For the purposes of this study, we defined allogrooming as one adult using one or more hands and/or teeth to pick through and brush aside an adult partner's fur. We classed the following as self-directed behaviours (SDB): self-scratching; self-grooming; self-biting; whole body shake; yawning (see Table 1 for definitions).

A focal female was chosen at random, using a random number generator, with a replacement generated if the focal female was out of sight. We recorded the occurrence and duration of all instances of SDB exhibited by the focal female using a stop-watch until the subject participated in an allogrooming bout with another adult female. At this point, we recorded the identity of the grooming partner and the direction of grooming (i.e., the identity of the initiator). If the focal female did not engage in allogrooming within 20 minutes a new focal female was sampled and the data were not included in subsequent analysis. If the focal female engaged in allogrooming with another adult female, the five minutes immediately preceding this was used as pre-grooming phase data.

An allogrooming bout was considered terminated if a break lasting over 30 seconds occurred. If a bout of allogrooming lasted for a minimum of 60 seconds, we then carried out a post-grooming observation; if it was less than 60 seconds, we did not count this as an allogrooming bout but continued focal observations as described above. Upon cessation of allogrooming, we continued to observe the focal female for a further 10 minutes, and recorded the durations of all instances of SDB exhibited by the focal female for the first five minutes. Post-grooming observations were abandoned if the focal animal engaged in further allogrooming within a 10-minute period of ceasing allogrooming. This ensured no data were

used to represent both post and pre grooming behaviour. Once the 10-minute post-grooming observation period ended, we sampled a new focal female.

We recorded the time and date of the post-grooming observation, and a five-minute Match-Control (MC) observation was undertaken at the same time for the same individual on the next available day, where we recorded the durations of all instances of SDB carried out by this individual. We postponed matched controls if the animals were fed during the scheduled time or if the subject engaged in an allogrooming bout in the five minutes prior to or after the observation.

We collected proximity network data using instantaneous scan sampling, once per hour, excluding times when individuals were being fed. During each scan we recorded the identities of all adult females that could be seen. For each of these individuals, we recorded the identity of all adult females within 1m of them, and defined these as being associated.

## **2.4 Data analysis**

We calculated the rate of SDB as events per minute for each five-minute sampling period (pre- and post-groom, and MC, excluding any time when the individual was out of sight – this was always less than one minute per five minute sample) and the duration of SDB as the mean number of seconds per minute spent engaged in SDBs. All analyses were carried out in R 4.4.1(R Core Team, 2021).

### *2.4.1 Does participation in allogrooming have a significant effect on self-directed behaviour?*



To determine which factors predicted SDB duration and rate across individuals, we fit linear mixed effects models using the package nlme (Pinheiro et al., 2021). The rate and duration data did not fit any commonly used distribution and so were transformed to approximate a gaussian distribution by a square root and Tukey's transformation (using the package Rcompanion, Mangiafico, 2022) respectively.

We used the transformed rate or duration of SDB as the outcome variable, gaussian as the family, Phase (pre-, post- grooming bout or MC), Role (whether the individual was recipient or initiator of the bout) and the Phase\*Role interaction as fixed factors and female ID as a random factor. We built models using all biologically relevant combinations of fixed factors (Table A1) and selected the best model based on AIC (Akaike Information Criterion; Akaike, 1974); the best model had the lowest AIC and was at least delta AIC 2 from the second-best model (Burnham & Anderson, 2002). We checked the fit of the best model by examining Q-Q plots following recommendations by Zuur & Ieno (2016).

To determine specifically whether SDB duration or rate significantly changed following allogrooming within individuals we employed a Wilcoxon signed rank test on matched pairs of pre- and post-grooming data.

#### *2.4.2 Association between social bond strength and post-grooming SDB*

To determine whether dyads with a greater social bond strength experienced a greater reduction in stress following an allogrooming bout than those with a lower bond strength, i.e. to determine whether there is a greater benefit of allogrooming for more strongly bonded individuals, we used a Spearman's rank correlation to test for an association between the focal individual's post-grooming SDB (measured by both median rate and median duration; medians were used to avoid the influence of outliers) and the bond strength with that

particular grooming partner (measured by the dyad's Half-Weight Index from the proximity matrix – see section 2.4.3).

#### *2.4.3 Association between social network position and baseline stress levels*

To build a proximity network using association data from scan samples, we calculated the Half-Weight Index (HWI; Cairns & Schwager, 1987) for each dyad to account for times when not all individuals could be seen (Whitehead, 2008). We defined an association as two individuals being within 1m of each other during a scan sample. Both undirected and directed grooming networks were also built based on total counts of allogrooming events observed within dyads (with the undirected version being based on the total number of allogrooming events and the directed version being based on which individual initiated an allogrooming session).

To determine whether proximity between individuals predicts grooming frequency, thus justifying the use of proximity as a measure of social bond strength, Quadratic Assignment Procedure (QAP) tests were carried out between the grooming network (both undirected and directed versions separately) and the proximity network. These were carried out using the package *statnet* (Handcock et al., 2016) using 10,000 permutations. This procedure carries out linked permutations of rows and columns of the observed matrix in order to generate multiple permuted matrices, which are then correlated with the dependent matrix in turn to calculate the probability that an observed correlation is significantly higher than expected (Krackhardt, 1988).

Social network position for all females in the proximity network was calculated by using three different measures: node strength, eigenvector centrality and closeness centrality. Node

strength is essentially the number and strength of an individual's direct relationships; it takes into account both the number of individuals directly linked to the individual in question and the weighting of these ties (Wasserman & Faust, 1994). Eigenvector centrality measures both the number and connectedness of an individual's social partners; a high eigenvector centrality value indicates that the individual has a large number of strong ties with individuals who in turn also have a high number of strong ties (Wasserman & Faust, 1994). Closeness centrality focuses more on how well connected an individual is within its network, including both direct and indirect connections; this measure can therefore be used to quantify an individual's potential influence on the group (Wey et al, 2008). We calculated weighted versions of these three centrality values; the package *igraph* (Csardi & Nepusz, 2006) was used to calculate eigenvector centrality and the package *tnet* (Opsahl, 2009) was used to calculate both node strength and closeness centrality.

We estimated baseline stress levels for each female using the median rate and duration of SDBs carried out across all MC observations. The median value was chosen after scrutiny of the data, to avoid the analysis being skewed by outliers. To determine whether social network position was associated with baseline stress levels, we used a Pearson's or Spearman's correlation test (dependent on variable distribution) to test for an association between centrality (using each of the three measures separately) and median MC SDB rate or duration.

### 3. Results

Analyses were based on 63 pre-post-MC triads (33 in which the focal female was the initiator and 30 in which the focal female was the recipient of allogrooming), giving a total of 189 (mean per female  $\pm$  SE:  $27.7 \pm 2.6$ ) focal samples. A total of 162 group scans was carried

out. The mean  $\pm$  SE number of grooming bouts recorded per F-F dyad was  $3.2 \pm 0.7$ . The majority of SDB was either scratching (N=201, 50.3% of total SDB events) or self-grooming (N=164; 41% of SDB events; 95.9% of total SDB time).

### *3.1 Does participation in allogrooming have a significant effect on self-directed behaviour?*

The best models for the predictors of both SDB rates and durations included Phase (MC, pre- or post-allogroom) as a fixed factor and ID as random variable (see Table A1 for model selection results). Role (whether an individual was the recipient or initiator of allogrooming) was not included in the best models. SDB rates and durations were significantly lower during the pre- and post-allogrooming Phases than in the MC samples (Tables 2 and 3; Figure 1).

The duration ( $V = 1159.5$ ,  $p = 0.039$ ), but not rate ( $V = 694$ ,  $p = 0.168$ ), of SDB significantly decreased within individuals following an allogrooming bout.

### *3.2 Association between social bond strength and post-grooming SDB*

Of the 21 possible dyads, two were never seen in proximity and four were never seen to engage in an allogrooming bout with each other. The proximity network significantly correlated with both the undirected and directed versions of the grooming network (QAP test: proximity vs. undirected grooming network,  $r = 0.85$ ,  $P < 0.001$ ; proximity vs. directed grooming network,  $r = 0.68$ ,  $P < 0.001$ ; Figure 2), thus justifying proximity as a measure of social bond strength.

There was no significant association found between the focal individual's post-grooming SDB and the bond strength with that particular grooming partner for either SDB measure (rate of SDBs:  $r_s(5)=0.033$ ,  $p=0.900$ ; duration of SDBs:  $r_s(5)=-0.121$ ,  $p=0.645$ ).

### 3.3 Association between social network position and baseline stress levels

There was a significant strong positive correlation between individual node strength and median MC SDB duration (Pearson's  $r_p(5)=0.867$ ,  $p=0.011$ ). However, there was no significant correlation between either eigenvector centrality or closeness centrality and median MC SDB duration (eigenvector centrality:  $r_p(5)=0.714$ ,  $p=0.071$ ; closeness centrality:  $r_p(5)=0.517$ ,  $p=0.235$ ). There were no associations between centrality values and median MC SDB rates (eigenvector centrality: Spearman's  $r_s(5)=-0.120$ ,  $p=0.799$ ; node strength:  $r_s(5)=0.259$ ,  $p=0.575$ ; closeness centrality:  $r_s(5)=-0.279$ ,  $p=0.545$ ).

## 4. Discussion

Both groomers and recipients significantly decreased the time spent engaging in SDB immediately following a grooming session. Both the rate and duration of SDB were lower immediately before and after a grooming bout than during MC sessions, sampled at the same time on a subsequent day. There was no effect of a grooming dyad's social bond strength on post-grooming SDB rates or durations, but we found a positive correlation between number and strength of an individual's social connections and median SDB duration.

The reduction in SDB duration immediately following a grooming bout, supports the tension-reduction function of allogrooming (Terry, 1970) in this group of lion-tailed macaques, for both grooming participants. This proximate mechanism has been proposed as a way of ensuring allogrooming is intrinsically rewarding (eg. Schino & Aureli, 2009), thus facilitating it as a behaviour to establish and maintain social bonds (Dunbar, 1988). This ultimately enhances reproductive success (Silk et al., 2003), possibly as a consequence of enduring relationships with related and unrelated grooming partners (Nakamichi & Yamada, 2007).

When measured as a rate, there was no significant decrease from pre- to post-grooming levels of SDB, in fact there was very little variation in SDB rates across all phases and individuals. In contrast, wild Barbary macaques' self-grooming duration increased post-grooming compared to match-controlled sessions, but the frequency of self-scratching did not change (Molesti & Majolo, 2013). Similar results have been reported in captive, free-ranging Barbary macaques, with higher self-scratching rates after grooming bouts than overall mean levels (Semple et al., 2013), although no comparison of duration was made. Potential explanations for an increase in self-scratching include frustration at the termination of a rewarding experience (Schino et al., 1988), stress at being exposed to potentially aggressive conspecifics (Castles et al., 1999), and increased self-scratching rates due to a change in behaviour, rather than an increase in anxiety (Buckley & Semple, 2012; Diezinger & Anderson, 1986). The Barbary macaque and lion-tailed macaque are both classified as tolerant, egalitarian species, as opposed to the highly hierarchical, nepotistic Japanese macaque, and the even more tolerant black crested macaque (Thierry et al., 2000) and so differences in social structure cannot be used as an explanation for the Barbary macaque being the only macaque species to show an increase in the rate of SDBs post-grooming. It could be, however, that free-ranging and wild macaques experience greater stress upon the cessation of grooming when compared to captive groups. These conflicting results also show the importance of methodology; although the majority of our data was comprised of self-scratching or self-grooming, it is possible that pooling several SDBs as we have, gives different results to focussing on one. In addition, the vast majority of empirical evidence published on the effects of grooming on anxiety levels in primates has focused solely on the rate of, rather than time spent engaging in, SDBs; our results show that the measurement of SDBs as a rate and as a duration do not necessarily give the same results.

We found no effect of role (whether an individual receives or gives grooming) on SDB rates or durations, suggesting that groomers also benefit directly from the grooming bout. Japanese macaques (Schino & Alessandrini, 2015) and black crested macaques (Aureli & Yates, 2010) also both show lower self-scratching rates after giving grooming, than during match-control

sessions but no direct comparison was made with pre-grooming levels. In female Barbary macaques, the length of grooming time given is negatively associated with faecal glucocorticoid metabolites (Shutt et al. 2007); in crested black macaques, self-scratching rates are lower after an individual has given grooming than in match-control periods (Aureli & Yates, 2010); and SDB rates in Japanese macaques decrease after giving grooming to an affiliated (but not unaffiliated) partner (Ueno et al., 2015). Intensive grooming has been recorded immediately after intergroup conflict in wild vervet (Cheney, 1992) and samango monkeys (Payne et al., 2003), again suggesting that giving grooming may help reduce tension.

Our finding that both SDB rate and duration are lower immediately before and after a grooming bout than during MC periods suggests that grooming may not occur when individuals are at their most stressed and supports the argument that animals choose to groom when already relaxed (Semple et al., 2013). Another possibility is that SDB acts as a communicative signal to other group members (Whitehouse et al., 2016) and individuals approach to groom only when SDB is below a certain level.

We found no effect of social bond strength on the effectiveness of allogrooming in reducing SDB. This suggests it may be the act of allogrooming itself that is more important in reducing stress rather than the particular relationship with the grooming partner. It has been suggested that giving grooming to affiliated partners is more self-rewarding than giving to unaffiliated partners, based upon a greater reduction in self-scratching following bouts of grooming with a more affiliated partner (Ueno et al., 2015). This idea is supported by evidence of bystanders of an aggressive encounter being more likely to seek subsequent grooming interactions with an affiliated partner than a non-affiliated partner (Judge & Mullen, 2005). It's possible that grooming for lion-tailed macaques is equally rewarding in reducing stress, regardless of partner. However, our study population was small, with high levels of relatedness between members, so it is possible that we did not have enough variation in social bond strength to reveal an effect. In larger populations with a greater range of kin and non-kin an effect of individual may be seen.

This study also found that the most connected individuals experience the greatest stress levels, since node strength was strongly positively correlated with the median duration of SDB. This could suggest that these individuals are more likely to experience lower welfare levels, and should be closely monitored by keepers. However, given the small study group, these results should be interpreted with some caution. No correlation was found between SDB rate or duration and closeness or eigenvector centrality; both these measures take into account indirect connections. Perhaps unsurprisingly in a small group of captive zoo animals, there is very little variability in the eigenvector centrality, suggesting that each adult female has an equal number of partners who themselves have the same number of partners (Wasserman & Faust, 1994). The fitness consequences of indirect connections can be significant, as social relationships between individuals rely on their own interactions, as well as those between their partners' social partners (Cheney & Seyfarth, 2007). Eigenvector centrality is positively associated with reproductive output (number of offspring produced) in rhesus macaques, (Brent et al., 2013), and with offspring survival in chacma baboons (Cheney et al., 2016). It is therefore thought to be beneficial for adult females to spend time in the proximity of others who also, in turn, spend time near others. Further study of a larger number of groups of lion-tailed macaques is needed to determine the importance of indirect connections in this species in captivity. We didn't explore the effect of dominance rank on SDB but lion-tailed macaques are thought to be amongst the most tolerant of macaque species (Thierry et al., 2000, although see Singh et al., 2006 for counter argument), and a study of 10 macaque species found no effect of dominance structure on grooming network measures (Balasubramaniam et al., 2018).

In this study, we highlight a potential benefit of allogrooming in lion-tailed macaques in terms of its stress-reduction function. We also illustrate how social network analysis can be used to quantify individual-level welfare by showing that individual network position correlates with the rate of SDBs and therefore individual stress levels. We suggest that these results, despite being



limited to one captive group, be considered when making decisions regarding the captive management of this and other related species.

### **Declaration of Competing Interest**

The authors report no declarations of interest.

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## Tables

**Table 1:** Ethogram of behaviours defined as self-directed behaviours for the purposes of this study.

Self-directed behaviour	Definition
Self-scratching	Rubbing or scraping at own skin or fur, with own hands or feet. Instantaneous, bout lasts

	less than 3 seconds.
Self-grooming	Using one or more hands, and/or teeth, to pick through and brush own fur. Bout lasts longer than 3 seconds.
Self-biting	Using teeth to bite at own skin or fur, with high intensity. Focussed on one area of the body.
Whole body shake	The individual's body rapidly shudders.
Yawning	Individual tilts head back and opens mouth wide, exposing teeth

**Table 2:** Median (IQR, inter-quartile range) rate and duration of self-directed behaviours, across all females and split by direction of grooming, during different Phases.

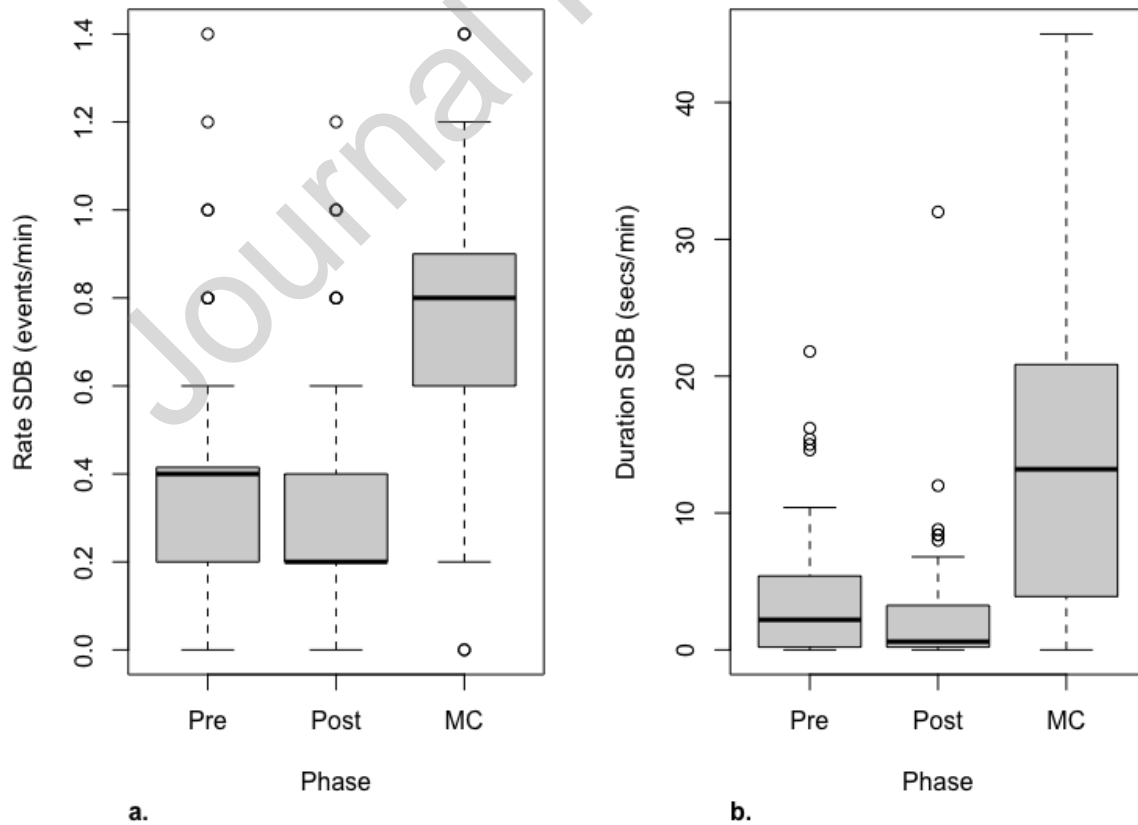
Phase	Rate (events/min)		
	Pre-grooming	Post-grooming	MC
All adult females	0.4 (0.2)	0.2 (0.2)	0.8 (0.3)
Initiator	0.4 (0.2)	0.2 (0.2)	
Recipient	0.4 (0.2)	0.2 (0.2)	
	Duration (secs/min)		
All adult females	2.2 (5.2)	0.6 (3.1)	13.2 (17.0)
Initiator	2.0 (5.0)	0.4 (4.8)	
Recipient	3.4 (5.4)	0.8 (2.2)	



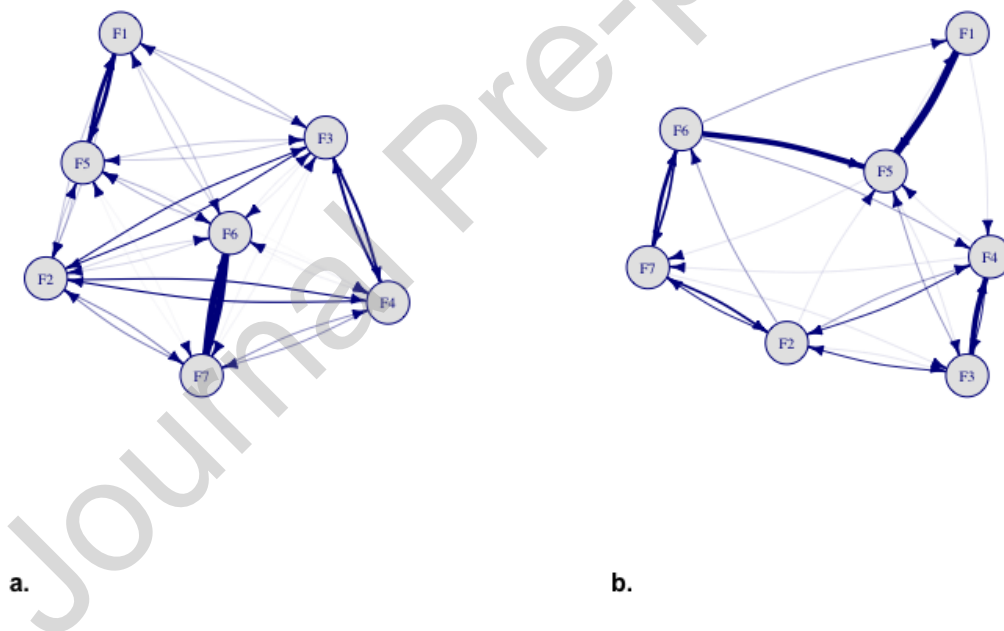
**Table 3:** Results from best linear mixed-effects models showing effects of Phase on the rate and duration of self-directed behaviour in lion-tailed macaques. The Phases pre- and post-grooming are compared with the Match-Control baseline factor. SE = standard error.

Outcome	Phase	Effect size	SE	t-value	p-value
Rate	(Intercept)	0.824	0.033	25.333	<0.001
	Pre-grooming	-0.267	0.046	-5.801	<0.001
	Post-grooming	-0.331	0.046	-7.198	<0.001
Duration	(Intercept)	1.952	0.087	22.510	<0.001
	Pre-grooming	-0.776	0.123	-6.334	<0.001
	Post-grooming	-0.989	0.123	-8.063	<0.001

**Figure captions**



**Figure 1.** Differences in individual **a.** rate or **b.** duration (per 5min period) of SDBs (Self-Directed Behaviours) between Phases (Pre = before allogrooming, Post = after allogrooming, MC = Match Control periods). The boxes are bounded by the upper and lower quartiles and are divided by the median. Maximum and minimum values within 1.5 box lengths of the quartiles are represented by the ends of whiskers and outliers are denoted by circles.



**Figure 2.** Networks based on **a.** proximity (where all individuals within 1m proximity of another individual were defined as being associated) and **b.** grooming (based on all allogrooming observations including focal individuals, with the arrows starting from the individual initiating allogrooming) for female lion-tailed macaques. Thickness of ties represents **a.** how frequently two individuals were observed in close proximity (weighted using the Half-Weight Index) and **b.** the absolute number of allogrooming interactions

observed within a dyad. Networks were visualised in the R package igraph using the graphopt layout algorithm.

## Appendix

**Table A1.** Models tested to determine factors predicting self-directed behaviour. Phase = pre- or post-grooming bout or MC(Match-Control), Role = whether focal individual was initiator or receiver of grooming. The best model is highlighted by bold type. Delta AIC shows the change in AIC value between each model and the best model.

Outcome	Fixed factors	Random factor	AIC	Delta AIC
Rate	<b>Phase</b>	<b>ID</b>	46.72	
	Phase + Role	ID	53.43	6.71
	Phase + Role + Phase* Role	ID	61.56	14.84
	Role	ID	91.47	44.75
Duration	<b>Phase</b>	<b>ID</b>	411.29	
	Phase + Role	ID	416.04	4.75
	Phase + Role + Phase* Role	ID	420.80	9.51
	Role	ID	468.29	57.00

### Conflict of Interest Statement

The authors declare no competing interest.

### Highlights

- Lion-tailed macaques reduce self-directed behaviour immediately after grooming.
- Self-directed behaviour also begins to decrease before allogrooming.
- This indicates that primates may allo-groom when they are already relatively relaxed.
- Grooming dyad social bond strength had no effect on self-directed behaviour.
- Females with more social connections exhibited higher median SDB.