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## Grooming interventions in female rhesus macaques as social niche construction

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Social animals invest time and resources into adapting their social environment, which emerges not only from their own but also from the decisions of other group members. Thus, individuals have to monitor interactions between others and potentially decide when and how to interfere to prevent damage to their own investment. These interventions can be subtle, as in the case of affiliative interactions such as grooming, but they can inform us about how animals structure their world and influence other group members. Here, we used interventions into grooming bouts in female rhesus macaques, Macaca mulatta, to determine who intervened in which grooming bouts, and what determined intervention outcomes, based on kinship, dominance rank and affiliative relationships between groomers and (potential) interveners. We show that high dominance rank of groomers reduced the risk of intervention. Bystanders, particularly when high ranking, intervened in grooming of their kin, close affiliates and close-ranked competitors. Interveners gained access to their close affiliates for subsequent grooming. Reduced aggression risk facilitated grooming involving three individuals, which was more common when a strong affiliative relationship existed and when interveners were lower in rank than the groomers. Thus, interventions in this species involved the monitoring of grooming interactions, decision making based on several individual and dyadic characteristics, and potentially allowed individuals to broaden their access to grooming partners, protect their own relationships and influence their social niche.

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Animals living in stable social groups daily navigate a web of social relationships with group members. Stable cooperative relationships with kin and nonkin, also called 'bonds', are a central feature in the lives of many species, and forming and maintaining them has a measurable impact on individual fitness (Ostner & Schülke, 2018; Silk, Cheney, & Seyfarth, 2013; Snyder-Mackler et al., 2020). Investment in bonds seems to enhance individual survival (Archie, Tung, Clark, Altmann, & Alberts, 2014; Ellis, Snyder-Mackler, Ruiz-Lambides, Platt, & Brent, 2019), infant survival (Cameron, Setsaas, & Linklater, 2009; Silk et al., 2009), access to mating partners (Städele et al., 2019) and food (Carter & Wilkinson, 2013; Samuni et al., 2018) and dominance rank attainment (Schülke, Bhagavatula, Vigilant, & Ostner, 2010). Individuals will invest time and resources (such as expended energy, access to

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food, increased risk during agonistic support) in forming bonds, which often remain stable across years (Kalbitz, Ostner, & Schülke, 2016; Massen & Sterck, 2013; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012).

Low-cost cooperative interactions, such as grooming in primates and allopreening in birds, are often thought to be the main mechanism for bond formation in animals (Seyfarth & Cheney, 2012). Group social structure changes with demographic and dominance hierarchy changes, and individuals may compete over access to cooperation partners (Noë & Hammerstein, 1995). Over time, this creates a risk for individuals: as their cooperation partners establish new alliances to third parties (de Waal & Luttrell, 1988), these partners may become less likely to cooperate with their old partner, reducing the benefits the individual gains in return for their investment (Mielke et al., 2017). Therefore, we would predict that individuals possess mechanisms to monitor cooperative interactions in their group that are potentially detrimental and try to influence them to their own benefit (Mondragón-Ceballos, 2001).

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Interactions involving third parties reveal animals as active agents gathering and evaluating information about their social network and shaping the lives of those around them (Schülke, Dumdey, & Ostner, 2020; Seyfarth & Cheney, 2015). This process of individuals influencing interaction patterns around them has been termed 'social niche construction' (Barrett, Peter Henzi, & Lusseau, 2012: Flack, Girvan, De Waal, & Krakauer, 2006: Rvan, Powers, & Watson, 2016): individuals' behaviour changes the social landscape of the group and the selective context in which social behaviour occurs. By affecting how group members interact with each other, individuals influence their own future interactions (Ryan et al., 2016). Studies on third-party influence in social animals have focused on agonistic interactions and bystanders' role in supporting opponents (Kajokaite, Whalen, Panchanathan, & Perry, 2019; Young, Majolo, Schülke, & Ostner, 2014), policing fights (Beisner & McCowan, 2013; Flack et al., 2006), reconciling participants (Cords & Aureli, 2000) and consoling victims (de Waal & van Roosmalen, 1979; Preis et al., 2018). Monitoring interactions of other agents and considering the social environment when making decisions increases the information processing involved in successfully navigating a social group in everyday life (Jolly, 1966).

In recent years, interest has moved towards sociopositive interactions, and the role bystanders play in changing partner choice (Mielke et al., 2018) and interaction outcome (Newton-Fisher & Kaburu, 2017). Bystanders can get involved by interfering in affiliative interactions of others. Previous studies have repeatedly shown that bystanders intervene in affiliative interactions if these are likely to change the actors' relationship with negative consequences for the bystander, either because a new bond is formed or the bystander's bond is challenged. In feral horses, Equus caballus, individuals are more likely to disrupt affiliative interactions if one partner is a close affiliate (Schneider & Krueger, 2012; VanDierendonck et al., 2009). In dogs, Canis lupus familiaris, play interventions target the player that is currently subordinate in the play bout, independent of relationship status (Ward, Trisko, & Smuts, 2009), and individuals show 'jealous' behaviour when their owner interacts with a dog model (Harris & Prouvost, 2014). In ravens, Corvus corax, paired individuals hold higher dominance status than unpaired individuals, so interventions are used to disrupt new pair formation attempts (Massen, Szipl, Spreafico, & Bugnyar, 2014). Grooming interventions allow mandrills, Mandrillus sphynx, to restrict grooming access of lower-ranking competitors and limit alliance formation (Schino & Lasio, 2018). In stumptailed macaques, Macaca arctoides, play, grooming, contact sitting and affiliative body contact all see interventions (Mondragón-Ceballos, 2001). Sooty mangabeys, Cercocebus atys atys, and western chimpanzees, Pan troglodytes verus, intervene in grooming to prevent their bond partners and close-ranked competitors from forming new connections (Mielke et al., 2017), and conversely they choose grooming partners to minimize the threat of interventions (Mielke et al., 2018). This competitive function results in polyadic grooming enforcing existing grooming patterns, rather than giving individuals access to a wider grooming network (Girard-Buttoz et al., 2020).

Thus, across species, third parties influence sociopositive interactions and consequently the social niche an individual inhabits the same way interventions do in agonistic contexts. However, the number of species studied is still limited, and the impact of many relevant factors unexplored. For example, the role of kin relations in interventions is poorly understood: in theory, kin should not have to resort to interventions to protect affiliative relationships as cooperation among kin should be more stable than bonds among nonkin (Silk et al., 2010). However, not all kin dyads cooperate at above-expected levels (De Moor, Roos, Ostner, & Schülke, 2020), and in larger matrilines, kin could compete with each other for access to other related individuals, for example siblings fighting to gain access to their mother (Pollet & Hoben, 2012). Equally, we do not currently know how the ability of some species to groom polyadically influences grooming partner choice or the outcome of grooming interventions (Nakamura, 2003), even though polyadic grooming does not seem to widen the grooming network of chimpanzees and bonobos, *Pan paniscus* (Girard-Buttoz et al., 2020). In a previous study, we could not explore the factors driving the outcome of interventions because mangabeys never groomed with more than two individuals, while interventions in chimpanzees almost always led to triadic grooming (Mielke et al., 2017).

Here, we used rhesus macaques, Macaca mulatta, as a model to understand the decisions underlying grooming interventions. Female rhesus macaque societies are despotic (i.e. rank defines the outcome of most competitive interactions), intolerant (i.e. low levels of reconciliation and high levels of aggression) and structured in matrilines (i.e. kin structure influences rank attainment and cooperation; Thierry et al., 2008). However, despite the bias towards bonds with kin in rhesus macaques, nonkin bonds of females exist and impact individual fitness (Ellis et al., 2019). Grooming and similar low-cost forms of cooperation (Carter et al., 2020) are the most visible behaviours used to negotiate bond maintenance and formation, and are a vital mechanism to negotiate social relationships in female rhesus macaques (Balasubramaniam & Berman, 2017). Rhesus macaques distribute their grooming preferentially towards closely ranked group members, even in the absence of kinship, and high-ranking group members groom more and are groomed more than expected (Snyder-Mackler et al., 2016). Given its importance for bonding and rank effects in priority of access, we predict high-ranking individuals would use interventions as a form of competition to maximize their access to partners. Grooming takes time and happens in the open, with group members watching, potentially giving them a way to influence cooperative exchanges. Females monitor who is close when interacting with offspring (Semple, Gerald, & Suggs, 2009) and selectively attend to agonistic and affiliative interactions in their vicinity and particularly so if a close affiliate or a higher-ranking female is involved (Schülke et al., 2020). While rhesus macaques have been reported not to groom polyadically in some populations (Brent, MacLarnon, Platt, & Semple, 2013), our study group grooms in clusters of three or more regularly (C. Bruchmann, personal observation 2019).

By focusing on a group of females with known dominance ranks, affiliative relationships and kin relations, we can disentangle grooming interventions. We predicted that, owing to the despotic intolerant social structure of female rhesus macaques, rank plays an outsized role in deciding who can successfully intervene, but that the decision to intervene or not is driven by kinship and social bond strength between potential interveners and the groomers. Our models addressed the following four questions. (1) Which dyads are most at risk of grooming interventions? We predicted that interventions are more likely if the two groomers are low in rank (as more group members can supplant them) and are neither kin related nor have a high dyadic bonding index value (as interventions could be more successful in preventing bond formation). (2) If interventions occur, who intervenes? We predicted that individuals intervened when they outranked the groomers (because individuals of low rank would be supplanted), when they were close in rank to one of the groomers (to prevent alliance formation of competitors), or when they had a high bonding index with either groomer (to prevent bonding of their own partners). We did not expect individuals to increasingly intervene when their kin were grooming. (3) When intervening, which groomer did interveners target? We predicted that individuals would preferentially establish access to the higher-ranking groomer or their own bond partners. (4) What determines intervention outcomes? We predicted that interveners were more successful in gaining access to a grooming partner if they were high in rank, had a bond with either groomer or were kin of either groomer.

#### METHODS

#### Study Group and Observations

For this study, C.B. observed the 29 adult females aged above 3 years in one group of 39 rhesus macaques with a single adult male at the German Primate Center, Goettingen, Germany between January and March 2019. All individuals were identifiable by a tattooed four-number code on their chest and individual differences in fur coloration, size and natural markings. The group had free access to a 250 m<sup>2</sup> outdoor and a 48 m<sup>2</sup> indoor enclosure, were fed once a day with fresh fruit and vegetables, once with a cottage cheese and grain preparation and once with monkey chow and had ad libitum access to water from several faucets.

Data were collected using three different methods. Instantaneous group scans (Altmann, 1974) were used every 30 min to assess time spent in 1 m proximity, friendly body contact and grooming by all female - female dyads. Only one social activity with one partner was recorded per individual per scan. Priority was given to grooming over contact sitting and contact sitting over being in close proximity and if the subject was engaged in interaction with two partners in the same priority class, one partner was chosen randomly, alternating the right or the left partner. These data were used to calculate relationship indices (see below). In 311 scans, 7746 individual behavioural scores were recorded, i.e. the average scan had almost 25 of the 29 individuals. Between scans, we used event sampling (Altmann, 1974) to record the sequence of behaviours (i.e. interventions and their outcome) that unfolded around 1132 grooming interactions between two adult females where rank, kinship and relationship information were available for both groomers. Events were recorded starting with the first grooming event occurring anywhere in the group after the end of a scan. We made an effort to record simultaneously events that occurred in parallel but were constrained by visibility. Thus, there may be a bias towards more frequently occurring grooming partner constellations which, however, reflects the opportunity for the bystanders to manipulate their social network. As potential interveners, we recorded all adult females that were present in the smaller indoor compartment of the enclosure at the onset of the event. If the event occurred in the outdoor part of the enclosure, we recorded all females that had an unobstructed view of the event at its onset. We did not record the activity of the potential interveners, assuming this information will not introduce consistent bias; the identity and number of distracted individuals will vary randomly across bouts. Intervention was recorded for all behaviours that could affect the two grooming individuals including aggressive behaviours (shove, jump onto, pinch, growl, repeated growl, lunge, open mouth threat, push-pull, slap, stare and blocking the groomers by going in between them), affiliative behaviours (touch, kiss, groom present, grooming, body contact), neutral approaches and passing by at close range. The outcome of the intervention was recorded as effectively interrupting the grooming or not, and as yielding access to one of the grooming partners for active or passive grooming or contact sitting or none of these options. Observations of an event ceased when all participants departed the grooming location. A second observer used the third method, all-occurrence sampling (Altmann, 1974), to record agonistic interactions between adult females to establish the dominance hierarchy.

#### Ethical Note

This work followed the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching and adhered to standards as defined by the European Union Council Directive 2010/63/EU on the protection of animals used for scientific purposes. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The Ethics Committee of the German Primate Center approved this study (AZ E1-19) which was completely observational.

#### Variables

Dominance ranks were derived from normalized David's scores (De Vries, Stevens, & Vervaecke, 2006) calculated from a winner – loser matrix of 1311 decided dyadic agonistic conflicts where one partner only showed submissive behaviour (bared-teeth display, crouch, give ground) either spontaneously or in reaction to aggression by the other partner, which did not show submission.

The strength of the affiliative relationship between two females was assayed with a dyadic composite sociality index (DSI; Silk et al., 2013) with three components: the number of individual observations including grooming (total 1564), contact sitting (total 1570) and close proximity (<1 m; total 1412). The DSI was calculated by taking the dyadic values for each of the components and dividing them by the group mean; the three components were then added and divided by three. The grooming included in the DSI was taken from scans and therefore does not contain the same bouts as those used to assess grooming interventions. All components were positively correlated in row-wise Kendall's matrix correlations with 10 000 randomizations of the symmetric matrix columns in Mat-Man1.1 (Netto, Hanegraaf, & De Vries, 1993) at row-wise average tau of 0.38–0.44 and all P < 0.001. The DSI by definition has an average of 1 and increases as dyads have affiliation times that are larger than the average dyad in the group.

Maternal kinship data were available for all females from the stud book of the colony. Dyads were classified as close kin if  $r \ge 0.25$  and nonkin if r < 0.25. In this sample, kin had a median DSI of 2.5, while nonkin had a median DSI of 0.28. Thus, for all interpretations, kinship and the relationship index are not independent conceptually in this community, even though collinearity was not a problem in any of the models (see below).

#### Analyses

All models were fitted in R v4.0.0 (R Development Core Team & R Core Team, 2020) using the 'brms' (Bürkner, 2018) and 'Rstan' (Stan Development Team, 2020) packages. Posterior estimates were generated using the Hamiltonian Monte Carlo algorithm. We used 3000 iterations for two chains: chain convergence was assessed by visual inspection of trace plots (McElreath, 2018), showing no convergence problems. For all fixed effects in all models, we used weakly informative, normal priors (Lemoine, 2019). All continuous variables were z standardized (Schielzeth, 2010). The DSI relationship index was log transformed in all models as it was highly skewed. Variance inflation factors (VIF) were assessed to rule out collinearity problems (Field, Miles, & Field, 2012) using the R package 'car' (Fox et al., 2014). The maximum VIF for any model was 2.2, owing to the definition of individuals as higher and lower ranking and the inclusion of both their ranks in the model. For all models, we present the 95% credible interval.

#### Model 1: which grooming bouts faced interventions?

We tested whether certain characteristics make it more probable that a grooming bout sees an intervention. We fitted a Bayesian generalized linear multilevel model with a binomial response variable and logit link function. The response determined whether an intervention took place (N = 521) or not (N = 611). Data were structured to reflect the rank relations between the groomers. We included as random effects the identity of the higher-ranking and lower-ranking individuals, and defined variables by the same standard. Test predictors in this model were the ranks of the higher-ranking and lower-ranking individuals. We also included whether the groomers were kin and their DSI. We included the number of bystanders as a control variable and the log-transformed duration of the grooming bout as an offset term. We included random intercepts for the two individuals; as most dyads had only one grooming bout, we did not include an intercept for the dyad. We included random slopes for the rank of the partner within each of the identities, as well as the random slope for the DSI value of the dyad in each of them.

#### Model 2: which bystander intervened?

For grooming bouts with interventions, we tested which bystander intervened. Thus, for 521 grooming bouts, we had overall 11 368 data points representing possible interveners (mean 22 bystanders, range 5–27). Representing the relationships between three individuals in a model in a meaningful way is difficult without influencing model fitting based on the specific solution selected. In a previous paper (Mielke et al., 2017), two models were run, one structured by the rank relations of the groomers, and one structured by their bond with the potential intervener; however, that way, the results for dominance rank and social relationships were separated. Here, we tested for the impact of rank, kinship and affiliative relationship strength in one model, applying conditional logistic regression analysis (Kajokaite et al., 2019). If at least one individual necessarily intervened in each bout (as is the case in this model), then their rank and relationship to the groomers, etc. matter not only globally, but also in relation to all other bystanders in that bout. In conditional logistic regression analysis, the importance of each effect on the outcome is dependent on the values for all other available choices in this bout, as well as their overall value.

We implemented conditional logistic regression analysis in a Bayesian framework using the 'stan\_logit' function in the 'rstanarm' package (Goodrich, Gabry, Ali, & Brilleman, 2020). The outcome variable was binomial, whether a bystander intervened or not. Data were stratified by grooming bout identifier, so that all bystanders for a bout were tested against each other. As testing was conducted mainly within a bout, information about the two groomers did not vary and was not included in the model. For each bystander, we included as fixed effects their dominance rank, the relationship value they had with each groomer, the absolute rank difference they had with each groomer (to test whether they disrupt grooming of close-ranked competitors) and whether they were close kin with each groomer. Conditional logistic regressions are sensitive to sparse data (Greenland, Schwartzbaum, & Finkle, 2000), and we were therefore unable to include interaction terms in the model. We included the random intercept for the bystander identity.

#### Model 3: which groomer did interveners target?

For all grooming bouts for which a target could be identified (N = 411), we tested which of the two groomers was selected. The 'target' in this case is either the first individual the intervener grooms, or the groomer that is not supplanted or attacked by the intervener (Mielke et al., 2017). We again fitted a conditional logistic regression analysis, with each bout represented by the two groomers and their characteristics tested against each other. One groomer was always chosen (1), the other one not (0). Each data point was represented by the rank of the groomer (to test whether

individuals select the higher-ranking groomer as target), the DSI between groomer and intervener and whether they were kin related. We included a random intercept for the groomer identity, with slopes for the DSI and kinship.

#### Model 4: what determined intervention outcome?

Interventions can have different outcomes from the perspective of the intervener: no further grooming happens, grooming continues without them, or the intervener gains access to one or two grooming partners. In the absence of overt aggression in grooming interventions, as was the case here, the outcome is mainly determined not by the decision of the intervener, but by the willingness of the groomers to remain close to the intervener and participate in grooming with them. If neither groomer can tolerate the presence of the intervener, grooming ends; if one individual can tolerate the intervener's presence, these two individuals groom as a dyad; if both are comfortable close to the intervener, polyadic grooming can occur. This level of tolerance for polyadic grooming was a major difference between chimpanzees and mangabeys (Mielke et al., 2017). Here, we tested the outcome of grooming interventions from the perspective of both the groomers and the intervener: when do groomers stay or leave? When does an intervener gain access to a grooming partner or disrupt a grooming bout?

For all interventions where both groomers' behaviour was identifiable (N = 504), Model 4.1 tests for each of the two groomers whether they remained in the grooming bout (1, N = 742) or not (0, N = 266), based on their relationship to the intervener. We assumed that the choices of the two groomers were independent from each other. In 102 bouts, both individuals left; in 62, one individual left; in 340, both individuals remained in the grooming bout postintervention. We fitted a generalized linear mixed model with binomial error distribution. As fixed effects, we included the ranks of the groomer and the intervener and the intervener. As random effects, we included the intercepts ID of the groomer and the intervener and the intervener.

Model 4.2 tested for each grooming intervention which of the following outcomes were achieved: the intervener was ignored and grooming continued (N = 211), the bout was entirely disrupted (N = 102) or the intervener gained access to at least one grooming partner (N = 191). We fitted a multinomial logistic regression, again using the 'brms' and 'rstan' packages, using each of the three outcomes as possible response. As fixed effects, we included the intervener rank, a factor indicating whether the intervener was kin with either groomer, and a continuous variable indicating the maximum DSI they had with either groomer. As a random effect, we included the identity of the intervener.

#### RESULTS

#### Which Grooming Bouts Faced Interventions? (Model 1)

There was only weak evidence for an impact of any test predictors on whether a grooming bout was subject to interventions, evidenced by the fact that none of the test predictors consistently showed credible intervals excluding zero (see Table 1 for posterior distributions of fixed effects). We found weak evidence that with increasing dominance rank of the higher-ranking and lowerranking groomers, the probability of an intervention was reduced. The odds ratios (OR) showed that one standard deviation increase in the rank of the higher-ranking groomer reduced the odds of intervention by a factor of 0.82, and for the lower-ranking groomer by a factor of 0.83. However, the credible interval shows that there

Table 1
Results for Model 1, testing which grooming bouts received interventions

	Estimate	Estimate error	Q2.5	Q97.5	Odds ratio estimate
Intercept	-0.35	0.11	-0.58	-0.13	0.71
Rank of higher-ranking groomer	-0.20	0.13	-0.46	0.05	0.82
Rank of lower-ranking groomer	-0.19	0.12	-0.42	0.05	0.83
Relationship strength of groomers	-0.08	0.11	-0.29	0.13	0.92
Kinship of groomers	-0.11	0.25	-0.60	0.37	0.89
Number of bystanders	0.16	0.08	0.01	0.31	1.17

Posterior estimates and 95% credible interval are given for all fixed effects, and the odds ratio for the estimates. Q2.5 and Q97.5 are the lower and upper bound of the credible interval; the further this interval is from 0, the more evidence we have for an effect of the predictor.

was considerable uncertainty around this estimate because the interval includes zero for both predictors. There was little evidence that the relationship index or kinship of the groomers influenced intervention likelihood. The full model explained a medium portion of variance in incidence of intervention with  $R^2 = 0.48$  (Gelman, Goodrich, Gabry, & Vehtari, 2019).

#### Which Bystander Intervened? (Model 2)

Several test predictors strongly influenced which of the bystanders intervened in grooming bouts (Table 2). The likelihood of intervening increased with bystander dominance rank, with a rank increase of one standard deviation increasing intervention likelihood by 76% (OR = 1.76; Fig. 1a). The rank difference between bystander and the higher-ranking groomer had no effect. Individuals were more likely to intervene the closer they were in rank to the lower-ranking groomer (OR = 0.73), with the plot of rank differences against fitted values (Fig. 1b) indicating that this mainly concerns individuals next in rank, while larger distances might be dominated by the absolute rank of the intervener. The more closely affiliated with either the higher-ranking (OR = 1.94; Fig. 1c) or lower-ranking groomer (OR = 1.60) bystanders were, the higher their probability of intervening. Bystanders that were kin of either groomer were also more likely to intervene (OR = 1.47 and 1.91; Fig. 1d). The full model explained 9% of the variance in incidence of bystander intervention ( $R^2 = 0.09$ ).

#### Which Groomer did Interveners Target? (Model 3)

Testing which of the two groomers the interveners sought to gain access to (Table 3), we found that they tended to target the groomer with whom they had a stronger affiliative relationship; one standard deviation increase in the relationship index increased the likelihood of choice by 35% (OR = 1.35). There was no support for a bias towards higher-ranking groomers or kin. Together these predictors explained 13% of variance in the response ( $R^2 = 0.13$ ).

#### What Determined Intervention Outcome? (Model 4)

We tested what determined the outcome of the intervention, that is, whether groomers avoided the intervener and left the scene or remained to continue the grooming bout (Model 4.1, Table 4). Decreasing the intervener's dominance rank strongly increased the likelihood that groomers stayed (OR = 0.65; Fig. 2a), especially with increasing groomer rank (OR = 1.17), while the interaction between the two terms did not strongly affect staying likelihood. With increasing affiliative relationship strength between the groomer and the intervener, groomers were more likely to stay (OR = 1.32, Fig. 2b). There was no evidence that kin relations to the intervener informed groomers' decision to leave or stay. The effect size of this model was  $R^2 = 0.10$ .

For Model 4.2, we reversed the question and tested what determines whether the intervener was ignored by the groomers (i.e. the original pair continued grooming without the intervener), disrupted the grooming bout (i.e. the grooming bout is over) or gained access to at least one grooming partner (i.e. the grooming bout continued including the intervener, either dyadically or with more than two individuals). There was consistent evidence that with increasing affiliative relationship strength with at least one groomer, interveners were more likely to gain access to at least one grooming partner (OR = 1.50) rather than be ignored (Table 5). At the same time, close affiliates were less likely to disrupt the bout than be ignored (OR = 0.70; Fig. 3a). An increase of one standard deviation of intervener dominance rank increased the likelihood of disrupting the bout rather than being ignored by 41% (OR = 1.41; Fig. 3b). These results mirror those of Model 4.1.

#### DISCUSSION

In this study, we examined how multiple individual and relationship characteristics (dominance rank, kinship and affiliative relationships) influence decisions about interventions in female rhesus macaque grooming. Our analyses showed that in this group of rhesus macaques, high-ranking females faced fewer interventions, could intervene more and were more likely to gain

#### Table 2

Results for Model 2, testing which bystanders intervened in grooming bouts

	Estimate	Estimate error	Q2.5	Q97.5	Odds ratio estimate
Rank of bystander	0.56	0.12	0.33	0.80	1.76
Rank difference to higher-ranking groomer	0.02	0.07	-0.13	0.17	1.02
Rank difference to lower-ranking groomer	-0.32	0.11	-0.53	-0.11	0.73
Relationship strength of bystander with higher-ranking groomer	0.66	0.06	0.54	0.79	1.94
Relationship strength of bystander with lower-ranking groomer	0.47	0.06	0.36	0.58	1.60
Kinship of bystander with higher-ranking groomer	0.39	0.16	0.07	0.69	1.47
Kinship of bystander with lower-ranking groomer	0.64	0.18	0.29	0.99	1.91
Rank of bystander Rank difference to higher-ranking groomer Rank difference to lower-ranking groomer Relationship strength of bystander with higher-ranking groomer Relationship strength of bystander with lower-ranking groomer Kinship of bystander with higher-ranking groomer Kinship of bystander with lower-ranking groomer	0.56 0.02 -0.32 0.66 0.47 0.39 0.64	0.12 0.07 0.11 0.06 0.06 0.16 0.18	0.33 -0.13 -0.53 0.54 0.36 0.07 0.29	0.80 0.17 -0.11 0.79 0.58 0.69 0.99	1.76 1.02 0.73 1.94 1.60 1.47 1.91

Posterior estimates and 95% credible interval are given for all fixed effects, and the odds ratio for the estimates. Q2.5 and Q97.5 are the lower and upper bound of the credible interval; the further this interval is from 0, the more evidence we have for an effect of the predictor.



**Figure 1.** Impact of (a) the bystander rank, (b) the rank difference between the bystander and the lower-ranking groomer, (c) the relationship index of the bystander and the groomers and (4) the kinship between bystander and groomers on intervention likelihood (Model 2). The continuous variables on the *x*-axes were *z*-transformed. Plots visualize predicted likelihood of intervention for observed data points, with lines obtained by locally weighted smoothing of the values.

#### Table 3

Results for Model 3, testing which groomer was targeted by intervention

	Estimate	Estimate error	Q2.5	Q97.5	Odds ratio estimate
Rank of groomer	0.08	0.11	-0.13	0.30	1.08
Relationship strength between groomer and intervener	0.30	0.12	0.06	0.55	1.35
Kinship of groomer and intervener	0.11	0.24	-0.35	0.59	1.12

Posterior estimates and 95% credible interval are given for all fixed effects, and the odds ratio for the estimates. Q2.5 and Q97.5 are the lower and upper bound of the credible interval; the further this interval is from 0, the more evidence we have for an effect of the predictor.

access to grooming partners. Kinship and affiliative relationships influenced interventions in their own way, motivating interventions and facilitating access to grooming partners. Being able to manipulate the social interactions and potential relationships of other group members gives animals considerable influence over their own fate in groups of interdependent agents. This is a process of social niche construction: individuals modify the selective context, here, the social interactions of other individuals in the group in which they have to make adaptive decisions (Ryan et al., 2016). While we know more and more about the ability of animals to monitor relationships between others (Berthier & Semple, 2018; Schülke et al., 2020), the question remains how flexible they are in employing this knowledge to their own immediate gain and to manipulate interactions between others. In an aggressive context, policing (Beisner & McCowan, 2013; Flack et al., 2006), agonistic intervention (Barrett et al., 2015) and third-party reconciliation (de Waal & van Roosmalen, 1979; Wittig & Boesch, 2005) have been described as ways for individuals to influence group members. This study adds to the increasing evidence that similar strategies exist for affiliative behaviour (Massen et al., 2014;

#### Table 4

Results for Model 4.1, testing whether groomers stayed part of the grooming bout

	Estimate	Estimate error	Q2.5	Q97.5	Odds ratio estimate
Intercept	1.15	0.15	0.85	1.45	3.17
Rank of groomer	0.16	0.11	-0.04	0.37	1.17
Rank of intervener	-0.43	0.15	-0.73	-0.15	0.65
Kinship of groomer and intervener	-0.01	0.25	-0.52	0.49	0.99
Relationship strength between groomer and intervener	0.27	0.11	0.05	0.49	1.32
Rank of intervener * rank of target	-0.02	0.11	-0.24	0.19	0.98

Posterior estimates and 95% credible interval are given for all fixed effects, and the odds ratio for the estimates. Q2.5 and Q97.5 are the lower and upper bound of the credible interval; the further this interval is from 0, the more evidence we have for an effect of the predictor.



**Figure 2.** Impact of (a) the intervener's dominance rank and (b) the relationship index between intervener and groomer on whether groomers stayed as part of the grooming bout after an intervention (Model 4.1). Continuous variables on the *x*-axes were *z*-transformed. Plots visualize predicted likelihood of intervention for observed data points, with lines obtained by locally weighted smoothing of the values.

# Mondragón-Ceballos, 2001; Schneider & Krueger, 2012; Ward et al., 2009).

Through a series of models, we explored which grooming dyads faced interventions, which individuals intervened, which groomer the intervener tried to gain access to and what determined intervention outcomes. To understand the wealth of results, it pays to focus first on the main difference in grooming intervention patterns previously found between sooty mangabeys and chimpanzees (Mielke et al., 2017). In mangabeys, grooming is never triadic, so all interventions were disruptive, which favoured high-ranking individuals and allowed them to manipulate grooming bouts of close affiliates and closely ranked competitors. This also seems to be the case in stumptailed macaques (Mondragón-Ceballos, 2001) and mandrills (Schino & Lasio, 2018). In chimpanzees, almost all interveners joined the grooming bout, as polyadic grooming is common (Nakamura, 2003), making intervention success independent of rank. Who decided to intervene, however, did not seem to differ between species; what differed was the ability of multiple individuals to be engaged in the same interaction. Rhesus macaques in our study group showed both joining (making the grooming bout polyadic) and disruptive interventions, allowing us to test what determined the outcome of grooming interventions.

We found broad similarities between our results on rhesus macaques and previous results on affiliation interventions in other species. As in mangabeys and mandrills (Mielke et al., 2017; Schino & Lasio, 2018), high-ranking bystanders were more likely to intervene, as they were less likely to be ignored than low-ranking interveners. Consequently, high-ranking grooming dyads saw slightly fewer interventions overall. Rank therefore seemed to confer power to individuals in deciding when to groom and intervene (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Sambrook, Whiten, & Strum, 1995). As in mangabeys and chimpanzees, bystanders were more likely to intervene when the lower-ranking groomer was close to them in rank, potentially to disrupt bond formation of closely ranked competitors (Mielke et al., 2017). Bystanders were more likely to intervene when they had strong affiliative relationships with either groomer, as in horses (Schneider & Krueger, 2012), mangabeys and chimpanzees. Kinship with either groomer also played a strong role. Like mangabeys and chimpanzees, our subjects did not seem to target the higher-ranking groomer as a subsequent grooming partner (Mielke et al., 2017). Note, however, that the absence of males in the study group might influence patterns of interventions and makes it difficult to evaluate how representative these patterns are for rhesus macaques more widely.

The consistent finding across species of individuals influencing affiliative interactions of their own bond partners raises questions as to how interventions relate to the evolution of jealousy (Harris & Prouvost, 2014). To establish the presence of friendship or romantic jealousy in humans observationally, we would test how we prevent partners from establishing new connections and renewed commitment with the partner (Aune & Comstock, 1991). Losing a close affiliate affects the life of animals with long-lasting bonds and having a 'warning system' to detect and the behavioural means to prevent such loss might prove valuable. Initial results with chimpanzees suggest that individuals show agitation and increased levels of aggression when close partnerships are threatened by affiliative interactions (Webb et al., 2020). We also currently do not know how long-term partner defection influences individual fitness.

We found that rhesus macaques used interventions to gain access to close affiliates, in contrast to mangabevs and chimpanzees. which did not preferentially groom their affiliates after intervention (Mielke et al., 2017), and domestic dogs, which targeted the receiver of play aggression when intervening (Ward et al., 2009). Strong affiliative relationships with either groomer increased the likelihood of grooming access postintervention, as groomers were less likely to leave. Thus, rhesus macaque females stop affiliates from grooming others and get access to them for additional grooming. These two functions are not mutually exclusive and targeting affiliates could indeed function to repair potential damage to the relationship. Alternatively, low-ranking individuals might use their affiliative and kin relationships to intervene in grooming bouts and access partners that they would not be able to, based on rank alone. An indication for this is that individuals were more likely to intervene if they were genetically related to either groomer. At the same time, kin were not more likely to be targeted by interventions or to remain part of the grooming bout postintervention. Interveners were more likely to gain access to grooming bouts if they had an affiliative relationship with at least one groomer and many of the subsequent grooming bouts were polyadic. Interventions might therefore function to increase an individual's grooming network, by using close affiliates and kin to access other group members, again shaping individuals' own social niche.

These results shine another light on the importance of affiliation between more than two partners. In many primate species, dyadic grooming seems to be the norm or only option. However, this artificially limits access to grooming partners: if individuals were able to groom with more partners at the same time, many of the time restrictions that are thought to underlie competition for grooming partners (Sambrook et al., 1995) would disappear. Some species, such as chimpanzees and bonobos, regularly groom as clusters (Nakamura, 2003; Sakamaki, 2013), which could allow individuals to maximize their access to preferred grooming partners even if these are already occupied (Girard-Buttoz et al., 2020); this seemed to be the case in the rhesus macaque group we studied here. However, this seems not to be a universal pattern for this species (Brent et al., 2013). The question is what underlies this

#### Table 5

NENTIN 101 WOULE 47. LENTING WHELTER STOUTHING THE VEHILUUS LENTINEU III UNTIDUUUL AULENS TU A STOUTHEL UL DEUTS ISTUUE	Results for Model 4.2	testing whether grooming	g interventions resulted in disru	uption access to a groomer or being ignored
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	Estimate	Estimate error	Q2.5	Q97.5	Odds ratio estimate
Intercept: access	0.04	0.24	-0.43	0.52	1.04
Intercept: disruption	-0.85	0.23	-1.29	-0.40	0.43
Access: kinship of intervener with either groomer	-0.37	0.28	-0.91	0.18	0.70
Access: rank of intervener	0.07	0.18	-0.26	0.44	1.08
Access: maximum relationship strength with either groomer	0.41	0.16	0.11	0.72	1.50
Disruption: kinship of intervener with either groomer	-0.07	0.31	-0.68	0.53	0.93
Disruption: rank of intervener	0.34	0.16	0.03	0.68	1.41
Disruption: maximum relationship strength with either groomer	-0.36	0.16	-0.67	0.06	0.70

Posterior estimates and 95% credible interval are given for all fixed effects of Model 4.2. The reference category in this case is 'being ignored'. Q2.5 and Q97.5 are the lower and upper bound of the credible interval; the further this interval is from 0, the more evidence we have for an effect of the predictor.





**Figure 3.** Impact of (a) the maximum relationship index of the intervener with either groomer and (b) the intervener dominance rank on the outcome of the intervention (Model 4.2). Continuous variables on the *x*-axes were z-transformed. Spaghetti plots are of 400 model runs. Lines represent different draws of conditional effects of the model; white lines within the distribution represent the median of all draws. Predictors were z-standardized.

eschewal of polyadic grooming: whether this is a question of multiple individuals tolerating each other at a close distance (Jaeggi, Stevens, & Van Schaik, 2010), whether coordinating more than two individuals poses a cognitive challenge (Wacewicz, Żywiczyński, & Chiera, 2017), or whether keeping track of reciprocal exchanges becomes more difficult with increasing groomer numbers (Schino & Aureli, 2009). Here, individuals were more likely to remain and continue grooming if they were affiliated to the intervener or the intervener was low in rank; both conditions that reduce the likelihood of aggression. This is likely to lead to a polyadic grooming pattern of distantly ranked individuals and friends being part of the same grooming cluster (Girard-Buttoz et al., 2020). Thus, tolerance between individuals might be an important aspect underlying polyadic grooming, rather than potential cognitive difference between species. Sharing a grooming partner could therefore follow the same rules as the sharing of any other resource, such as access to food.

Theories regarding the evolution of cognitive abilities in animals often focus on the challenges posed by an ever-changing social environment and the need to track and adapt to the actions of other agents (Seyfarth & Cheney, 2015). Social bonds (Ellis et al., 2019) and indirect connections to third parties (Brent, 2015) are highly

relevant for rhesus macaques. Grooming is common and an important tool to navigate relationships (Balasubramaniam & Berman, 2017). Rhesus macaques track who is close to them (Semple et al., 2009) and what these individuals are doing (Schülke et al., 2020). Here, we have shown that rather than simply gathering information, they use their own behaviour to manipulate interactions between others to their own benefits and construct their own social niche. Females based their decisions during interventions on a number of characteristics of the groomers and their relationship to these individuals, but also potentially on triadic awareness of the relationship between the groomers (Kubenova et al., 2016; Wittig, Crockford, Langergraber, & Zuberbühler, 2014). Thus, this study presents additional evidence for the flexibility and cognitive skills primates use when navigating and shaping their social environment.

### **Data Availability**

Data and scripts are available at https://github.com/ AlexMielke1988/Mielke-et-al-Rhesus-Interventions.

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