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# Male Barbary macaques choose loyal coalition partners which may increase their coalition network betweenness

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## Abstract

Reciprocity in the form of contingent exchanges of goods and services is widespread across animals. While there is ample evidence for helping to be contingent upon the help received from a partner, less attention has been paid to partner avoidance based on harm inflicted by a partner. Here, we investigated whether partner choice for agonistic support against powerful targets is guided by loyalty received, i.e., the tendency to refrain from attacking the subject in a coalition with any third partner. We further assessed whether loyalty received by all cooperation partners may generate increased levels of betweenness in the coalition network of a group, a measure of indirect connectedness that has previously been associated with fitness benefits. Based on observational data from male coalitions against male group mates in Barbary macaques (*Macaca sylvanus*), loyalty received was found to predict the frequency of cooperation in coalitions and the loyalty given to a partner. We propose that loyalty-guided reciprocity will be favored in species with rank-changing coalitions where defection is particularly risky. The more loyal a male's cooperation partners were, the more central he was in the coalition network in terms of higher in betweenness, suggesting a cognitively simple strategy underlying complex network positioning. Analyses of simulated data suggest strong correlations of loyalty and betweenness to be more prevalent in the relatively small groups characteristic of many primate species.

KEYWORDS
betweenness, indirect connections, loyalty, macaques, partner choice, primates, reciprocity, social network

## 1 | INTRODUCTION

The role of reciprocity for the evolution and maintenance of cooperation has been debated for half a century. Debated issues often concerned calculated reciprocity (sensu Brosnan & de Waal, 2002), which is one specific mechanism that requires elaborate cognitive abilities (Carter, 2014; Nowak, 2012; Stevens & Hauser, 2004; Trivers, 1971). With the broad and inclusive original definition of reciprocity as "individuals exchanging goods and services that are contingent on each other" (Trivers, 1971), several different behavioral strategies and the psychological processes of the underlying cognitive mechanism become tractable for comparative studies with the promise to improve our understanding of their evolution (Schweinfurth & Call, 2019a). Here, we highlight two phenomena that are underrepresented in reciprocity research. First, help may not only be directed to those that help but also to those that refrain from inflicting harm and act loyal instead (de Waal & Luttrell, 1988; Silk, 1992). Second, partner choice may concern how the partner is connected to third parties in the wider social network. We use nonhuman primates (primates hereafter) as an example of animals living in medium-sized, relatively stable, cohesive, closed, and individualized groups.

Reciprocity is widespread across primate species (Packer, 1977; Schweinfurth & Call, 2019b). In more than two thirds of experimental studies the commodity provided to a partner was food which is, however, rarely shared in the wild (Jaeggi & Gurven, 2013). Therefore, correlational evidence of reciprocity from observational studies, particularly those from the wild, mostly concerns the services grooming and agonistic support (Schweinfurth & Call, 2019b). Grooming is reciprocally exchanged for grooming even after statistically controlling for preferential grooming of close kin (Schino & Aureli, 2010a) although the relative effects of nepotism and reciprocity are statistically difficult to quantify (Carter et al., 2019). Grooming exchanges are particularly well-balanced between the closest affiliation partners among philopatric females (Silk et al., 2009, 2010), philopatric males (Mitani, 2009), and post-dispersal, usually unrelated males (Kalbitz et al., 2016). The strength of affiliative relationships also predicts the probability to provide support in agonistic conflicts (Schino, 2007) which, together with experimental evidence of affiliation biased helping (Borgeaud & Bshary, 2015; Cheney et al., 2010; Cheney & Seyfarth, 1990), suggests that emotion-based integration of gives and takes across several acts of helping may underlie direct reciprocity in primates (Schino & Aureli, 2010b; Schweinfurth & Call, 2019b).

Notably, the exchange of agonistic support is one of the rare examples where partners are chosen not only for their previously demonstrated likelihood to reciprocate in kind to the subject but also for their demonstrated willingness to inflict harm on the subject or not (Silk, 1992). Chimpanzees have been described to employ a "revenge strategy", where individuals intervene in agonistic conflicts most often against those that aggressively intervene against them (de Waal & Luttrell, 1988). Another strategy for partner choice in polyadic agonistic conflicts is sensitivity to loyalty, i.e., to help those that do not interfere against you. Patterns of interventions in captive male bonnet macaques (*Macaca radiata*: Silk, 1992) are consistent with a preference for loyal partners. Building on this work, our first aim here is to investigate whether males of another macaque species, the Barbary macaque (*Macaca sylvanus*), also form more coalitions with males that are more loyal to them.

Male–male coalitions against other males, i.e., simultaneous aggression against a common target (de Waal & Harcourt, 1992), have been extensively studied in male Barbary macaques in large outdoor enclosures and in the wild in Morocco. Male Barbary macaques support kin more often than non-kin (Widdig et al., 2000). If presented with a choice of different partners during an ongoing conflict, males preferentially recruit the partner they share the closest affiliative relationship with (Young, Majolo, et al., 2014). This choice is rewarded as closer partners are less likely to refuse a call for help when they are recruited into a conflict (Young, Majolo, et al., 2014). Thus, close affiliation partners are reliable supporters. Males use coalitionary attacks to break up mating consortships of other males with consequences for relative mating success of males (Bissonnette et al., 2011; Kuester & Paul, 1992; Young et al., 2013). Furthermore, the ability to muster support affects dyadic dominance relationships (Berghänel, Ostner, & Schülke, 2011) to the degree that it promotes attainment and maintenance of high dominance rank (Young, Schülke, et al., 2014), which is generally associated with increased reproductive success in primate multimale groups (Ostner et al., 2008).

This leads us toward the second aim. The past decade has seen evidence mounting that it is not only interindividual variation in direct connectedness (e.g., number of coalition partners or frequency of coalitions formed with these partners) that is associated with fitness components but also variation in indirect connectedness within the wider social network across vertebrates (Brent, 2015; Ostner & Schülke, 2018; Snyder-Mackler et al., 2020). One aspect of indirect connectedness is an individual's role in connecting otherwise unconnected parts of the network quantified as betweenness centrality (Krause et al., 2015). Binary betweenness counts how often an individual lies on the shortest path between any two other individuals in the network (weighted betweenness further takes into account the strength of those paths). Therefore, the mechanisms underlying any betweenness effects on fitness are most tractable if costs or benefits are flowing through the network like information or infectious disease requiring contact or close proximity (Brent, 2015; Franz & Nunn, 2009; Hamede et al., 2009; Sosa et al., 2021). In the scarcely connected association networks of many birds, high betweenness centrality is associated with increased access to foraging information (Aplin et al., 2012) and social information which may promote social niche selection, i.e., individuals with more knowledge about different parts of the social network may be better able to concentrate their engagement on a part that provides them with most benefits (Oh & Badyaev, 2010; Ryder et al., 2008). If food is actively shared like in hunter-gatherer society, food can also be thought of as flowing through the network providing individuals with high betweenness with a strong buffer against shortages (Page et al., 2017). Yet, if foraging in cohesive groups where food is not shared, like most primates and many other mammals, most information will be almost equally available to all group members and disease quickly reaches all parts of the network via pronounced small world effects (Kasper & Voelkl, 2009; Newman, 2010). In medium-sized, cohesive, densely connected groups other mechanisms must mediate the association of betweenness with fitness.

Agonistic support features prominently not only among the proposed behavioral strategies promoting direct connectedness (Alberts, 2010; Cameron et al., 2009; Cheney, 2010; Schülke et al., 2010) but also has been put forward as a mediator of links between indirect connectedness and fitness (Gilby et al., 2013; Stanton & Mann, 2012). Betweenness in the agonistic support/coalition network of male chimpanzees is associated with increased paternity success and increased likelihood to attain the alpha position in the following year (Gilby et al., 2013). It has been suggested that male chimpanzees may gain high betweenness because they refrain from forming coalitions against males with whom they share many coalition partners (Gilby et al., 2013). Consequently, this work has been cited as evidence for the use of third-party knowledge and complex social cognition (Seyfarth & Cheney, 2015). A cognitively more parsimonious strategy would be that, instead of choosing coalition partners based on knowledge about their connectedness to others, subjects base their decision on how these partners intervene against them, i.e., how loyal they are, which may increase subject's betweenness as a byproduct. If loyalty underlies coalition formation, then by forming a coalition with an ally, the subject also prevents future coalition formation between the current ally and the current target as this relationship becomes disloyal due to the current action which should increase betweenness. There is little doubt that primates and other animals can make inferences about third party relationships from observations (Bergman et al., 2003; Kajokaite et al., 2019; Pazy-Mino et al., 2004; Seyfarth & Cheney, 2015). Yet, they may still use simpler rules of thumb if these produce similar outcomes (Bissonnette et al., 2009); in other words, while experiments show what animals can do, observational work has to demonstrate that they do do it. Thus, our second aim is to assess whether coalitionary loyalty is positively associated with betweenness in the coalition network. All measures of indirect connectedness (like betweenness) in a social network can be emergent properties. Therefore, it is important to always also assess effects of direct connectedness as an alternative explanation for correlations between an emergent indirect metric and any other variable as a control (third aim).

To address these aims, we first test with observational data on male Barbary macaques at Affenberg Salem whether males strategically choose loyal partners, i.e., form coalitions with those partners that do not form coalitions against them, by regressing the number of coalitions formed with a partner over an index that quantifies the loyalty received from that individual (Silk, 1992). We then assess correlations of individual betweenness in the coalition network with the loyalty a subject received from its partners. To more fully represent variation at the individual level, we summarize an individual's loyalty received from different partners with three different measures, average loyalty received, number of completely loyal partners, and number of completely disloyal partners. As a way of weighting this evidence against an alternative explanation, we also assess correlations of the three loyalty measures with the direct connectedness measure degree (number of partners in the coalition network). We use simulated networks to explore how variation in network size and number of observations per individual would affect the relative support for loyalty being stronger correlated to betweenness than degree.

## 2 | METHODS

### 2.1 | Data collection

We present analyses of data collected during two study periods in 2008, October–January (Berghänel et al., 2010; Berghänel, Ostner, Schröder, et al., 2011; Berghänel, Ostner, & Schülke, 2011) and 2014, September–November (Rathke et al., 2017). We studied one out of three groups of Barbary macaques that freely mingle year-round in a 20 ha forested enclosure at Affenberg Salem, Germany (https://www.affenberg-salem.de/en/). The animals were provisioned once a day with various fruits, vegetables, greens, and grain and have ad libitum access to monkey chow and water (de Turkheim & Merz, 1984). The study group was chosen, because it had been observed for a previous study on a related topic by a different research group in 2006 (Bissonnette et al., 2009). Given that (a) all males aged 5 years and older were included as subjects without the possibility to opt out of our study, (b) all individuals were mother-reared in large mixed-age groups and had been free to migrate between three groups, and (c) care was taken to spread observation effort equally across individuals (Table 1), our sample should represent a minimally STRANGE test sample (Webster & Rutz, 2020).

### 2.2 | Coalitions

We defined within-group male coalitions as simultaneous aggressive acts shown by at least two adult males against an adult male target (de Waal & Harcourt, 1992). We collected data on the identity of all males involved in such a polyadic interaction via focal animal sampling of all males (906 h in 2008 and 590 h in 2014, Table 1). In 2008, coalitions were also recorded ad libitum, with 2–3 parallel focal observers distributed over group spread. In 2014, a second observer collected additional data via event sampling (Martin & Bateson, 2007). During event sampling, the observer moved over the area of group spread and sought out situations where several males were close enough to potentially engage in male coalitions. The group had 23 adult males in 2008 (total group size 50) and 18 adult males in 2014 (total group size 67) ranging in age from 9–27 to 5–24 years, respectively. Between the study periods eight males died and nine immigrated from a neighboring group in the same continuous 20 ha enclosure or matured into the adult age class. We have previously shown that all males that aged from the adult age class into the post-prime phase of 14 years or older completely changed their coalitionary behavior; these males went from being among the top targets and least participants to being the least targets and the top participants in coalitions (Rathke et al., 2017). Thus, despite the fact that nine males were included in both coalition networks, we consider the two data sets to be independent samples. All but five males were immigrants in 2008. All focal animals were fully habituated to the presence of human observers and easily identifiable from their physical appearance in terms of locomotor patterns, posture, injuries, fur coloration, and facial pigmentation.

Our dataset consisted of 184 and 81 coalitions in 2008 and 2014, respectively. We excluded coalitions that involved more than two partners (34 in 2008 and 10 in 2014), because we could not judge whether a third male joined the other two because he supported only one or both of them.

**TABLE 1** Focal animals and observation hours by year of study, sorted by year of birth.

| Male ID | 2008 | 2014 |
|---|---|---|
| Y2 | 39.8 | |
| Z30 | 39.0 | |
| C5 | 39.8 | |
| C13 | 39.8 | |
| D10 | 39.0 | |
| D11 | 39.0 | |
| D13 | 39.0 | |
| D25 | 39.0 | |
| D29 | 39.0 | |
| E13 | 40.5 | |
| E14 | 39.0 | |
| F3 | 39.0 | |
| G4 | 39.0 | |
| H3 | 39.0 | 32.6 |
| I2 | 39.0 | 31.0 |
| J3 | 39.0 | 33.1 |
| L1 | 40.5 | 31.9 |
| M1 | 39.0 | 33.0 |
| N1 | 39.8 | 32.2 |
| N2 | 39.0 | 33.2 |
| O2 | 40.5 | 33.0 |
| O3 | 40.5 | — |
| Q7 | 39.0 | 32.8 |
| U1 | | 32.0 |
| W1 | | 33.3 |
| W4 | | 31.3 |
| Y3 | | 34.2 |
| Z1 | | 33.0 |
| Z3 | | 33.7 |
| A1 | | 34.4 |
| B3 | | 30.0 |
| B4 | | 35.2 |
| Mean | 39.4 ± 0.6 | 32.7 ± 1.2 |
| Total | 906 | 589.9 |

## 2.3 | Loyalty

For this study, we modified the loyalty index introduced by Silk (1992). We were unable to systematically differentiate between parallel coalitions and agonistic support (Bissonnette et al., 2011), i.e., we were not always sure about who supported whom in a coalition because the prelude to a coalition was recorded for 73% in 2008 and for 59% of coalitions in 2014 only. Therefore, we cannot score how often individual *A* joined an ongoing fight to help *B* (agonistic support *A* to *B*) versus how often *B* did the same for *A* (agonistic support *B* to *A*). We also lack the data density to analyze loyalty given from *A* to *B* depending on the identity of the target male *C* as done by Silk (1992). Thus, we modified the previously used loyalty index by Silk (1992) to an index $LI_{A\to B}$ that quantifies loyalty that male *A* expresses toward male *B* based on the number of observations $N_{A+B\to C}$ where they formed coalitions together (simultaneous attack, *A* supporting *B* or *B* supporting *A*) against any other male *C*, and the number of observations $N_{A+C\to B}$ where male *A* attacked male *B* together with any other male *C*:

$$LI_{A\to B} = \frac{N_{A+B\to C}}{N_{A+B\to C} + N_{A+C\to B}}$$

$LI_{A\to B}$ is zero (i.e., completely disloyal) if male *A* formed coalitions against male *B*, but was never observed to team up with *B*. In contrast, $LI_{A\to B}$ reaches 1 (i.e., completely loyal) if *A* only was observed forming coalitions with *B*, but never against *B*. The index is directional, i.e., $LI_{A\to B}$ is not necessarily equal to $LI_{B\to A}$, but varies with the number of coalitions against each other. The index is undefined, i.e., denominator is zero, if *A* neither cooperated in a coalition with an individual *B* nor received coalitionary aggression from *B*. We excluded from further analyses 47% and 68% of dyads for which the loyalty index was undefined. Since $N_{A+B\to C}$ includes both agonistic support provided from *A* to *B* and from *B* to *A* the loyalty index used here is always larger and perhaps less differentiated than the index used by Silk (1992).

## 2.4 | Reciprocity in loyalty

All analyses were run separately for the two study periods. To control for the complex random effects structure inherent in social network data (Hart et al., 2022), we ran the analyses on the dyadic level with Bayesian multi-membership models implemented in brms (Bürkner, 2017, 2018) running in stan (Stan Development Team, 2023) in R (R Core Team, 2023). We first modeled the number of coalitions formed with a partner as a response to the z-transformed loyalty received from that male (Poisson model) and then assessed the relationship between loyalty given to a partner and the loyalty received from that same male (Beta model). Since observation hours per male varied very little (Table 1) we did not include an offset term in the count model. We performed prior checks and used weakly informative priors (0, 1). We ran 4 chains with 4000 iterations each and 2000 warmups. All chains converged and Rhat = 1 for all intercepts and effects. Since the beta models did not accept values of 0 and 1 we used pseudo-values for these extremes and changed 0 to 0.001 and 1 to 0.999 which should not affect model outcomes. We used ggplot2 (Wickham, 2016) to visualize the data, model predicted values, and 90% credible intervals.

## 2.5 | Association of loyalty and betweenness

We were further interested in the association of a male's betweenness and several measures of the loyalty he received from others. To this end, we integrated the dyadic data at the individual level into three measures: we counted (1) the number of completely disloyal group mates (LI = 0), (2) the number of completely loyal partners (LI = 1), and then assessed (3) the average loyalty a male received from all his partners (mean LI). We then built binary coalition networks (Gilby et al., 2013) to calculate binary betweenness and degree in R 3.1.2 (R Core Team, 2023) using the *igraph* package (Csárdi & Nepusz, 2006). To evaluate the robustness of our results, we also calculated weighted betweenness in a network of the frequency of coalition formation with the package *Tnet* (Opsahl, 2009). The relationship of the three loyalty measures and betweenness (or degree) was assessed with simple Spearman correlations run in Statistica 13.5.0.17 (StatSoft Europe).

### 2.6 | Simulations of alternative explanation via network degree

In a final step, we used artificially generated coalition data to assess whether and how frequently loyalty can be more closely correlated to betweenness than to degree under different conditions which is relevant in the broader discussion of the relative importance of direct versus indirect connectedness (Brent, 2015). For this purpose, we generated 1000 random networks each for our parameter settings by sequentially pulling from all group members the first and second ally and a target. To make the simulations more realistic and to reflect the interindividual variation in the propensity to engage in coalitions, we assigned 20% of the individuals a 10 times lower chance of being pulled from the pool. The parameters we manipulated were network size, i.e., the number of nodes/individuals in the network (5, 10, 20, or 40) and the average number of observations per individual (2, 5 or 10). For each randomly generated network, we calculated and correlated to each other individual network degree, betweenness, and our three loyalty measures.

## 3 | RESULTS

Our analyses of 2 against 1 coalitions revealed that in both years all but one males formed coalitions against other males, yet individual strength (# of coalitions formed), degree (# of partners), and betweenness in the coalition network (# of shortest paths between any two individuals that passes through an individual) varied widely. Individual males formed 1–31 coalitions (mean ± SD = 14.3 ± 8.0) in 2008 and 1–21 (8.4 ± 7.9) in 2014 with up to 15 different partners (7.8 ± 3.2) in 2008 and up to 11 partners (4.1 ± 2.4) in 2014 with a maximum of 8 coalitions per partner (1.7 ± 0.5) in 2008 and a maximum of 9 coalitions per partner (1.8 ± 0.8) in 2014. Males were the target of a coalitionary attack up to 30 times (8.3 ± 9.2) in 2008 and up to 21 times in 2014 (4.2 ± 4.6) with 80% and 70% of attacks concentrated on the top six targets in 2008 and 2014, respectively (Figure 1).

### 3.1 | Loyalty

In both datasets, the more loyal a partner was to the subject, the more coalitions the subject formed with that partner (2008: mean ± SD of estimated fixed effect = 1.18 ± 0.12, 90% Credible Interval = 1.00–1.37; 2014: estimate 1.01 ± 0.14, CI = 0.77–1.25; Figure 2). This suggests that males refused helping those more often who inflicted more harm on them.

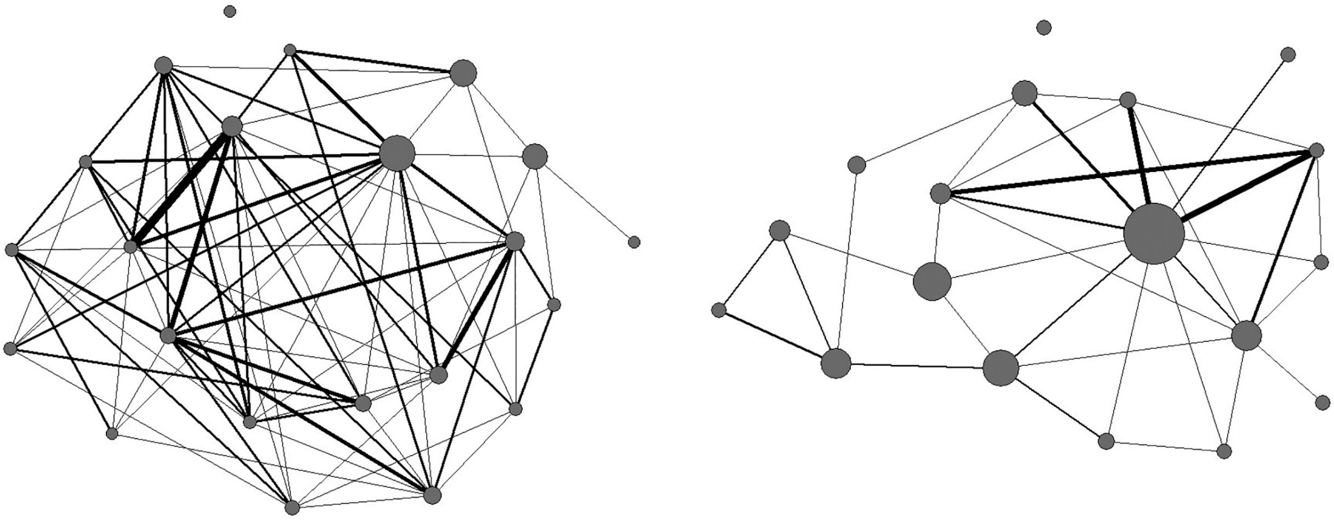

FIGURE 1 Coalition networks of male Barbary macaques in 2008 (left) and 2014 (right). Nodes represent individual males and edges represent the number of two-against-one coalitions two males formed against any other male. Node size is proportional to the binary betweenness of the male in the network.

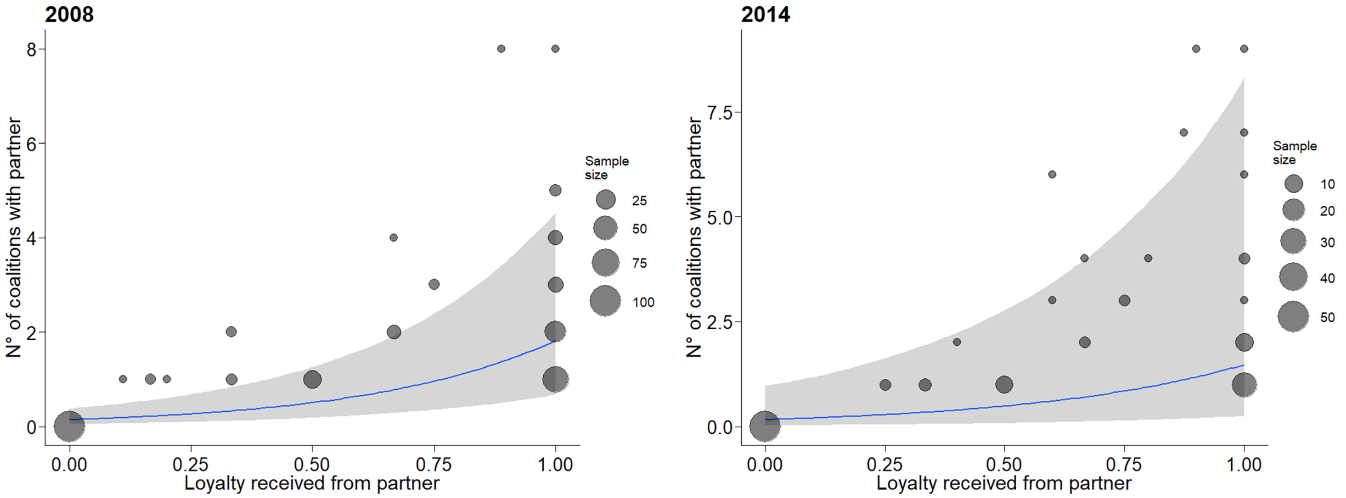

FIGURE 2 Distribution of coalitionary help across partners varying in loyalty (Loyalty Index) towards the subject in 2008 (left) and 2014 (right). The raw data (points) are plotted with a line representing the fitted values from a multimember brms model and the corresponding 90% Credible Interval.

## 3.2 | Reciprocity in loyalty

Males also acted more loyal toward those who were more loyal to them (2008: estimate fixed effect of z-transformed loyalty received = 0.71, CI = 0.54–0.89; 2014: estimate = 0.49, CI = 0.20–0.76). The more an established coalition partner refrained from inflicting harm on his ally the less harm he had coming his way from that ally. In all models, the probability that the effect was larger than zero exceeded 95%.

## 3.3 | Association of loyalty and betweenness

Further analyses on the individual level were run on binary betweenness to provide comparability with published work (Gilby et al., 2013). Binary betweenness is a simple count of how many shortest paths between any two individuals in the network run through a subject which ignores the weight of those connections. Yet, in the coalition networks explored here, binary and weighted betweenness were highly correlated (Spearman's $\rho_{2008} = 0.68$ $N = 23$, $\rho_{2014} = 0.65$, $N = 18$).

With correlations being slightly stronger in the smaller network in 2014, we found (1) that betweenness of a male in the coalition network was negatively associated with the number of males being completely disloyal towards him (LI = 0), i.e. males that formed coalitions against the focal male but never with him (Spearman's $\rho_{2008} = -.55$, $p < .05$; $\rho_{2014} = -.23$, $p > .1$; Figure 3, left panels). (2) Conversely, betweenness of a focal male increased with an increasing number of completely loyal partners, i.e., those that were partners to him and never formed a coalition against him (LI = 1 $\rho_{2008} = .41$, $p < .1$, $\rho_{2014} = .59$, $p < .01$; Figure 3, middle panels). On a more nuanced level, betweenness in the coalition network was also positively associated with the average loyalty (mean LI) a male received from all of his partners ($\rho_{2008} = .40$, $p < .1$, $\rho_{2014} = .57$, $p < .01$; Figure 3 right panels).

## 3.4 | Simulations of alternative explanation via network degree

As can be expected from the dyad level analyses, the three individual-level loyalty measures were also correlated to coalition network degree, i.e., the number of allies a male had, in both study periods. These correlations were stronger than the correlations with betweenness (degree/LI = 0: $\rho_{2008} = -.65$, $\rho_{2014} = -.40$; degree/LI = 1: $\rho_{2008} = .86$, $\rho_{2014} = .76$; degree/mean LI: $\rho_{2008} = .67$, $\rho_{2014} = .83$; all $p < .01$), which gains relevance in the discussion of direct versus indirect connectivity effects on fitness.

Analyses of simulated data suggest, however, that whether our three loyalty measures are more closely related to betweenness than to degree, depends on group size and the average number of coalitions observed per individual (Figure 4). For all loyalty measures, with decreasing group size betweenness was increasingly likely the stronger correlate compared to degree. In contrast, the effect of number of coalitions depended strongly on the loyalty measure. For the number of completely disloyal partners the observation number had a positive effect, for completely loyal partners the effect was negative and for average loyalty there was no apparent effect visible. In roughly a third of cases across all simulations, the loyalty a male received was more closely related to his network betweenness than degree.

## 4 | DISCUSSION

This discussion is structured into three parts. To provide context to the two findings of cooperation in coalitions increasing with partner loyalty and of a reciprocal relationship between loyalty given and received, we first discuss why loyalty as a cooperative behavioral strategy may evolve ultimately in species forming relatively large and stable groups. Then we discuss active linking as a cooperation

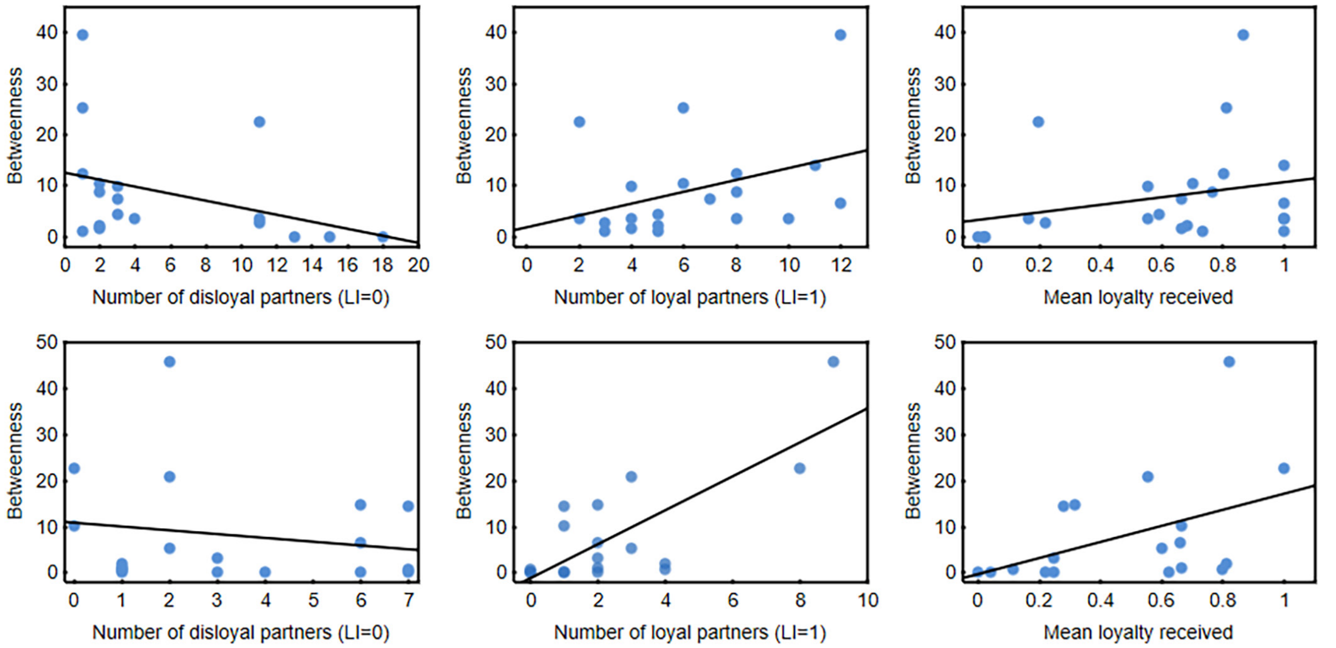

**FIGURE 3** Relationship of loyalty and betweenness in the coalition network in the two study periods (top row 2008, bottom row 2014). Plotted are individual binary betweenness measures over three measures of the loyalty a male received from other males; left: number of completely disloyal partners (Loyalty Index = 0), middle: number of completely loyal partners (LI = 1), right: average loyalty a male received from all his partners.

promoting mechanism enhancing cooperation in networks and that active linking may be at play in the formation of reciprocally loyal relationships. We end with discussing how the positive relationship between loyalty and betweenness may inform studies associating betweenness in coalition networks to fitness correlates vis-à-vis the alternative explanation via direct network connectedness.

Reciprocal agonistic support in within-group conflicts is a widespread phenomenon in mammals of both sexes (Bissonnette et al., 2014; Olson & Blumstein, 2009; Smith et al., 2010, 2022). Affiliation patterns often mirror the cooperation network (Ostner & Schülke, 2014), and individual males form coalitions or support each other in agonistic conflicts more often, the closer the affiliative relationship they share (Berghänel, Ostner, Schröder, et al., 2011; Mitani, 2006; Mitani et al., 2000; Schino, 2007; Watts, 2002). These are not mere spatial effects, but if given a choice, closely bonded partners are preferentially recruited as allies (Perry et al., 2004), and they are also more reliable than other partners in the sense that closely bonded partners less likely refuse to support a partner in a conflict when recruited (Young, Majolo, et al., 2014). In line with this, primates playing a trust game adjusted from human behavioral economics, trusted those more that they shared a close affiliative relationship with (Engelmann & Herrmann, 2016).

Loyalty may be yet another characteristic of close affiliative, cooperative, supportive relationships promoting reciprocity via emotional book-keeping across several interactions (Schino & Aureli, 2010b; Schweinfurth & Call, 2019a). Loyalty is expressed in the fact that one does not form coalitions against one's own ally and is a behavioral strategy, not a virtue (Silk, 1992). Being the target of a male coalition can cause injury, loss of resource access, or loss of status (van Schaik et al., 2004, 2006). Avoiding such costs imposed by others is a major adaptive problem (McCullough et al., 2013), and yet reciprocal partner choice based on harm avoidance has received little attention except for studies on punishment as a mechanism maintaining cooperation (Clutton-Brock & Parker, 1995; Zöttl et al., 2023). Even as an ally, males are at risk to pay significant costs, and engaging as an ally in rank-changing coalitions (van Schaik et al., 2006; Watts, 2010) is particularly risky. Dominance hierarchies based on fighting power will be reordered by those coalitions in a way that stronger males come to rank below their physical power rank. Shortly after a rank change, coalitionary support is needed as defense against retaliation by the former, now lower ranking, but still stronger target (van Schaik et al., 2006). Thus, allies in a rank-changing coalition require their partner to be reliable (i.e., come to aid when needed) and loyal (do not turn against them) at least in the short term (Ostner & Schülke, 2014). This argument is supported by the findings of this study showing that Barbary macaque males, who engage in rank-changing coalitions (Young, Majolo, et al., 2014), form more coalitions with more loyal partners. The function of male coalitions is less clear for bonnet macaques studied in a 0.2 ha enclosure, but they exhibited the same reciprocity in loyalty observed in Barbary macaques here (Silk, 1992). Yet, in two other macaque species (*M. mulatta* and *M. arctoides*) individuals intervened less against those that intervened more against them (de Waal & Luttrell, 1988). These findings do not contradict our hypothesis that loyalty is particularly important where rank-changing coalitions are prevalent, because these groups comprised mainly females (de Waal & Luttrell, 1988).

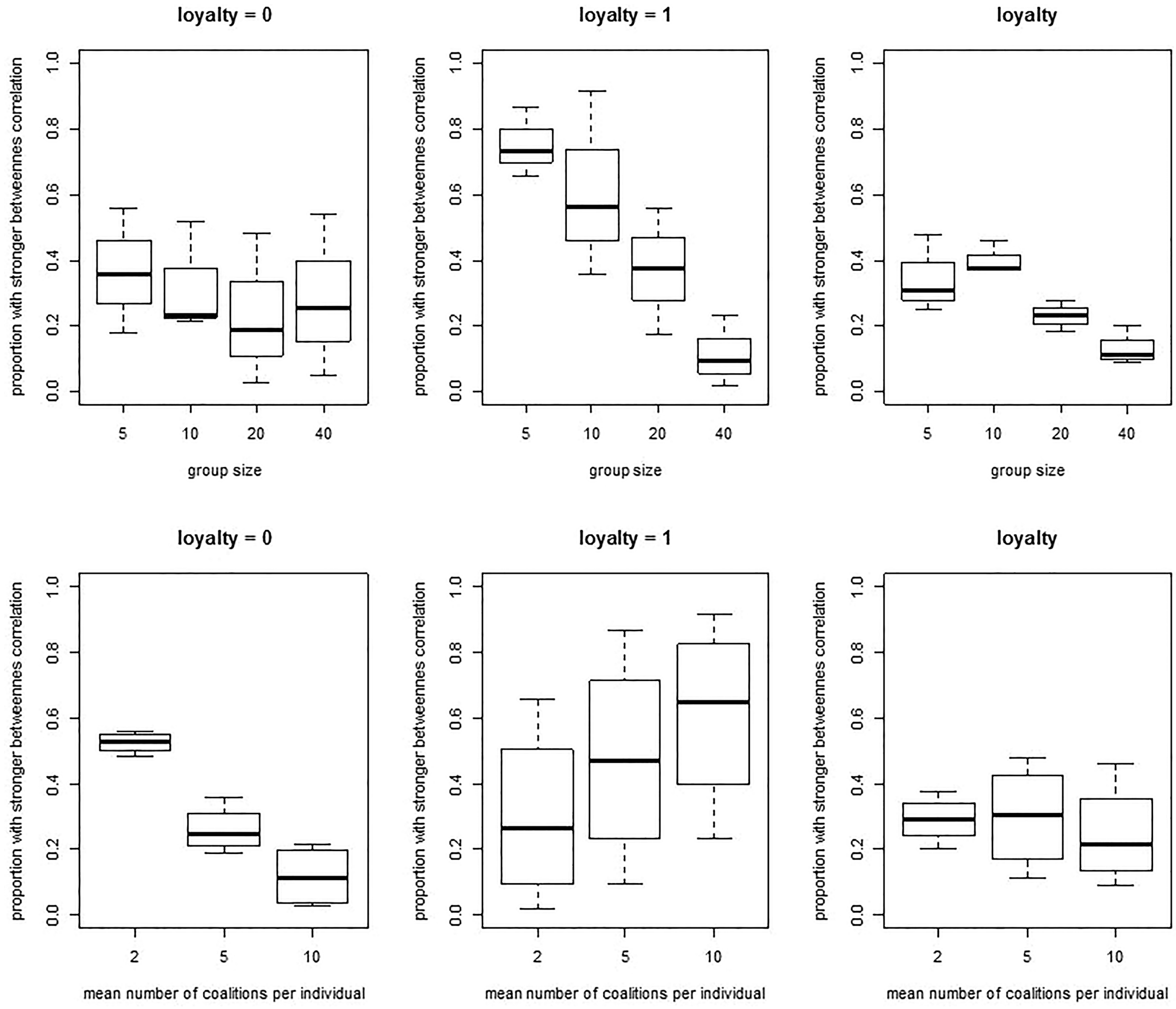

**FIGURE 4** Results of analyses of simulated data with top row different group sizes (5, 10, 20, 40 individuals) and bottom row different numbers (2, 5, 10) of observed coalitions per individual. Loyalty measures are from left to right the number of completely disloyal partners, the number of completely loyal partners, and the mean loyalty received from all partners. Box plots represent the median, interquartile range, and range of for the proportion of cases in which the correlation between a loyalty measure and betweenness was larger than the correlation with network degree.

Where affiliation is predictive of cooperation, males may estimate a partner's loyalty a priori from direct connectedness in the affiliation network (Ostner & Schülke, 2014). As an alternative or in addition, males may develop a set of loyal relationships by active linking. Theoretical and empirical work suggests that selective link breaking is an effective mechanism enhancing the evolution of cooperation on graphs (Fehl et al., 2011; Pacheco et al., 2006a, 2006b). A male will cooperate with a partner against others until his partner turns against him, which will lead to the male breaking his links with this partner (Fehl et al., 2011). In our study, coalitions were frequent enough to allow in theory for such dynamics with a median rate of 0.28/observation hour (Berghänel, Ostner, Schröder, et al., 2011), which equals 2.8 per day during short autumn and winter days and more than 300 coalitions per individual during the 4 months mating season. Although we currently cannot rule out that loyal partners assort by another mechanism than active linking, we expect similar dynamics to occur in other primates and mammals as well. Irrespective of the dynamics, helping loyal partners more will structure support networks as it leads to local assortment of loyal partners, and constrain both supporter and target choice.

In relation to the case of male chimpanzees where coalition network betweenness correlates with reproductive success and rank attainment (Gilby et al., 2013), it is important to note that chimpanzees can be vengeful (de Waal & Luttrell, 1988) and retaliate by negative reciprocity (Jensen et al., 2007). Although the same individuals refuse to pay for retaliation (Jensen et al., 2007), this shows that chimpanzees like other mammals (McCullough et al., 2013) are sensitive to the costs imposed on them by others and consider these costs when choosing partners. From our finding that betweenness is associated with loyalty received, it may be concluded that the competitive advantage of high betweenness in the coalition network of male chimpanzees could be a byproduct of helping loyal partners. To some degree, this interpretation appears inconsistent with the data because in the chimpanzee study fitness measures were more strongly correlated to betweenness than degree, whereas in the macaque data loyalty was more strongly correlated to degree than betweenness. Results of our simulations can help navigate this inconsistency.

In the simulated data, the probability to see a stronger correlation of loyalty and betweenness instead of degree never exceeds 0.5, but is close to 0.3 in many scenarios, i.e., can be expected in every third data set. Given that the number of males was much larger in the investigated macaque groups compared to the chimpanzee groups, it seems plausible that in chimpanzees loyalty might correlate more strongly with betweenness, and thus with the related fitness measures. If this holds true, then the observed competitive advantage of chimpanzee males with high betweenness could be an emerging rather than a causal effect. Although all indirect network measures are particularly sensitive to noise in small groups (Firth et al., 2017), it seems unlikely that reverberating effects of such noise on betweenness reliably yield correlations with other variables like loyalty. Alternatively, variation in betweenness may result from other simple social differences between individuals that do not concern with how many partners to interact how often, but that cause emergent effects in indirect connectivity much more reliably than in direct connectedness (Firth et al., 2017). Without providing a conclusive answer for the chimpanzee case, this study proposes a new, cognitively simple behavioral mechanism that can produce pronounced differences in social position with possible effects on individual fitness.

## AUTHOR CONTRIBUTIONS

**Oliver Schülke:** conceptualization, formal analysis, project administration, resources, supervision, writing original draft, writing—review & editing; **Eva-Maria Rathke:** conceptualization, data curation, formal analyses, investigation, grant acquisition, writing—review & editing; **Andreas Berghänel:** investigation, writing—review & editing; **Julia Ostner:** conceptualization, project administration, resources, supervision, writing—review & editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data underlying the analyses in this manuscript are available from the GöttingenResearchOnline data repository (GRO.data) https://doi.org/10.25625/WTHKIH, GRO.data, V1.

## ETHICS STATEMENT

The study was purely observational, strictly non-contact/non-invasive, and adhered to the guidelines for the treatment of animals in teaching and research of the ASAB Ethical Committee/ABS Animal Care Committee SAB (2023) and the EU directive 2010/63/EU.

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