

# Fitness benefits of coalitionary aggression in male chimpanzees

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**Abstract** Coalitionary aggression occurs when at least two individuals jointly direct aggression at one or more conspecific targets. Scientists have long argued that this common form of cooperation has positive fitness consequences. Nevertheless, despite evidence that social bond strength (which is thought to promote coalition formation) is correlated with fitness in primates, cetaceans, and ungulates, few studies

have directly examined whether coalitionary aggression improves reproductive success. We tested the hypothesis that among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*), participation in coalitionary aggression increases reproductive output. Using 14 years of genetic and behavioral data from Gombe National Park, Tanzania, we found that coalitionary aggression increased a male's chances of (A) siring offspring, compared to other males of similar dominance rank, and (B) ascending in rank, a correlate of future reproductive output. Because male chimpanzees form coalitions with many others within a complex network, we used social network analysis to identify the types of connections correlated with these fitness benefits. The beneficiaries of coalitionary aggression were males with the highest “betweenness”—that is, those who tended to have coalition partners who themselves did not form coalitions with each other. This suggests that beyond simply recognizing third-party relationships, chimpanzees may use this knowledge to choose coalition partners. If so, this is a significant step forward in our knowledge of the adaptive value of social intelligence. Regardless of mechanism, however, this is the first evidence of genetic benefits of coalitionary aggression in this species, and therefore has important implications for understanding the evolution of cooperation.

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## Introduction

Coalitionary aggression (a “coalition”) occurs when at least two individuals jointly direct aggression at one or more targets (Harcourt and de Waal 1992), and is particularly common in social, large-brained species (Smith et al.

2010). Behavioral ecologists have long assumed that this common form of cooperation has positive fitness consequences. For example, coalitions are thought to be a primary reason why individuals form long-term affiliative bonds (Silk 2007)—e.g. grooming partners are more likely to form coalitions, which are, in turn, assumed to increase fitness (Seyfarth 1977, Silk et al. 2003, Muller and Mitani 2005, Mitani 2009). Nevertheless, despite growing evidence that social bond strength (based upon spatial association and/or grooming preferences) is correlated with fitness in several taxa, including primates (Silk 2007, Silk et al. 2010), cetaceans (Frère et al. 2010) and ungulates (Cameron et al. 2009), very few studies have directly tested whether coalitionary aggression increases reproductive success.

There are at least two ways in which coalitions could increase fitness. First, there has been a long-standing assumption that coalitions are important for attaining higher dominance rank (Chapais 1992, Muller and Mitani 2005, Silk 2007), which is positively correlated with reproductive success in many species (Silk 2002), including chimpanzees (*Pan troglodytes* (Wroblewski et al. 2009)). There is suggestive qualitative evidence supporting this hypothesis. In one group of rhesus macaques (*Macaca mulatta*), coalitions among subordinates appeared to be instrumental in the expulsion of the alpha and beta males (Higham and Maestriperi 2010). There are also three accounts of a male chimpanzee becoming alpha as a result of coalitionary support from other males (Riss and Goodall 1977, de Waal 1982, Nishida 1983). However, two (de Waal 1982, Nishida 1983) of these rank ascensions took place in unusually small social groups, and it is impossible to know whether or not they would have occurred in the absence of coalitions. To date, the only quantitative data come from a 2-year study of Assamese macaques (*Macaca assamensis*), in which coalition rate was positively associated with future dominance rank, which in turn, was correlated with reproductive success (Schülke et al. 2010).

A second possible benefit of coalitions is that they increase the probability of a male siring offspring, independently of rank. For example, male fallow deer (*Dama dama*) with high coalition rates mated more often than expected for their rank (Jennings et al. 2011). This was also observed for frequent supporters of the alpha male chimpanzee of the Kanyawara community in Kibale National Park, Uganda (Duffy et al. 2007). There is also a report that describes 12 cases in which coalitionary mate-guarding among high-ranking male chimpanzees was associated with increased male mating probability (Watts 1998). In these three studies, however, it is unknown whether coalitions resulted in a greater number of sired offspring. Mate-guarding alliances increased the mating success of male bottlenose dolphins (*Tursiops* spp., Connor et al. 1992), but males without allies were also able to sire offspring (Krützen et al. 2004). In Camargue horses (*Equus caballus*), subordinate males that

formed coalitions with a dominant male had higher reproductive success than other low-ranking males (Feh 1999).

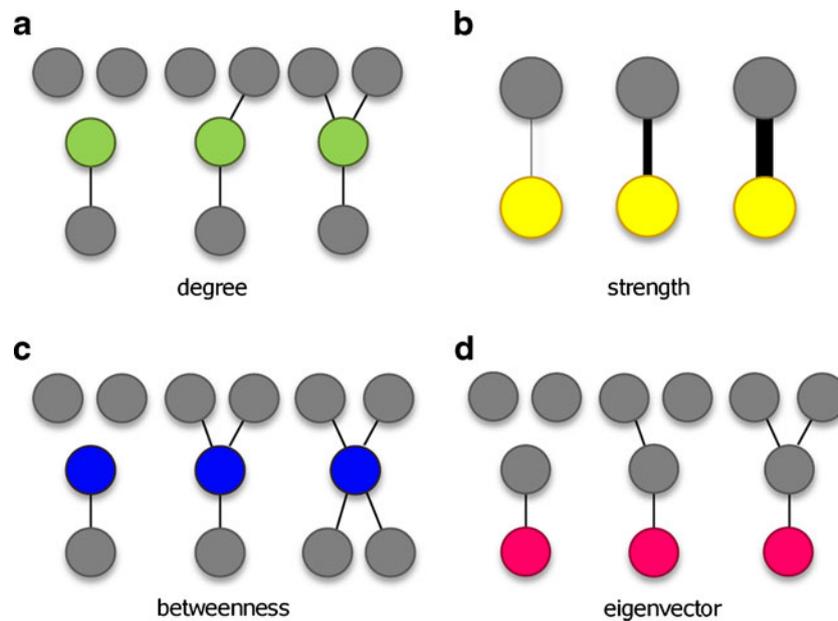
We used 14 years of genetic and behavioral data on wild chimpanzees (*Pan troglodytes schweinfurthii*) from the Kasekela community in Gombe National Park, Tanzania to test the hypotheses that male coalitionary aggression leads to positive fitness benefits via increased (1) dominance rank and (2) reproductive output. We build upon previous studies by (1) examining a longer time frame, (2) using genetic paternity data and (3) utilizing social network analysis. Social network analysis is increasingly used to determine how associations (e.g., proximity, mating, grooming) within large, fluid social groups affect an individual's health (Christakis and Fowler 2007), reproductive success (McDonald 2007) and social influence (Flack et al. 2006). We used four standard measures of network centrality, which quantify an individual's position in the network relative to all others (Wasserman and Faust 1994). (1) Degree is equal to the number of individuals with whom a subject formed a coalition (Fig. 1a). (2) Strength is a measure of coalition frequency (Fig. 1b), and is equal to the sum of a subject's dyadic coalition rates. (3) Betweenness is equal to the number of shortest connections between other males that passed through a subject (Fig. 1c). A male with high betweenness had more coalition partners who did not form coalitions with each other than a male with low betweenness did. (4) Eigenvector centrality is equal to the number of direct as well as indirect coalition partners. Males with high eigenvector centrality had many coalition partners, who in turn had many partners themselves (Fig. 1d). Degree, eigenvector centrality and betweenness are based on binary data (presence/absence of at least one dyadic coalition), while strength is based on weighted (frequency) data.

Our general prediction was that one or more of these metrics would be positively associated with the probability of increasing in rank and/or siring offspring. However, the critical distinction between the four metrics is that degree and strength consider only the individuals a subject interacts with directly, while eigenvector centrality and betweenness also allow us to take indirect connections into account (Brent et al. 2011)—e.g., the interactions among an individual's coalition partners. As such, eigenvector centrality and betweenness stress partner identity (Brent et al. 2011). Therefore, the relative importance of each measure for predicting fitness had differing and important implications regarding the process by which males choose coalition partners.

## Methods

### Behavioral data

The Kasekela chimpanzee community in Gombe National Park was first habituated to the presence of researchers in



**Fig. 1** Schematic representation of social network metrics. *Circles* (“nodes”) represent individuals. *Lines* (“connections”) represent social interaction between two individuals. *Colored nodes* represent the individual of interest (the “subject”), *gray nodes* represent other members of the social group. Network metrics increase for the subject from left to right. **a** Degree: the number of individuals with whom the subject interacts. In the current study, subjects with high degree have many coalition partners. **b** Strength: the rate at which the subject interacts with others. Here, *line thickness* represents the frequency at which two individuals interact, with thickness increasing with the frequency of interaction. Subjects with high strength form coalitions frequently with others. **c** Betweenness: the total number of shortest paths (routes of

connections that can be followed on a graph from one node to another) that pass through the subject linking members of the social group to each other. The *subject on the left* (low betweenness) does not link any other members of the social group to each other, while the *subject on the right* (high betweenness) lies along the shortest path that links each member of the social group to each other. Subjects with high betweenness tend to have coalition partners that do not form coalitions with each other. **d** Eigenvector centrality: a measure of both the number and quality of a subject’s social partners. Subjects with high eigenvector centrality, have many coalition partners, who themselves have many coalition partners

the 1960s. Pairs of Tanzanian field assistants have conducted full-day focal follows of adult chimpanzees using the same protocol since the 1970s (Goodall 1986). Using checksheets, one assistant keeps a continuous record of the composition of the subgroup with which the focal individual is traveling. The second assistant keeps a narrative record of the behavior of the focal chimpanzee as well as conspicuous behaviors (including aggression and coalitions) exhibited by any member of the subgroup. These data are archived, digitized, and organized into a relational database at the Jane Goodall Institute Research Center at Duke University.

We used 14 years of these data (1995–2008) for which genetic information was also available (see below), divided into seven 2-year periods. Our subjects were males who were at least 12 years old (the youngest age at which a male in this community is known to have sired offspring; Wroblewski et al. 2009) by the beginning of a given period and still alive at the end (9–11 males per period, 16 individuals, Table S1). On average, individual males were observed for 2,475.7 h in a 2-year period with little variation in time observed between males (mean coefficient of variation = 0.16, range 0.10–0.25), thus avoiding sampling bias (Croft et al. 2008).

From the narrative notes, we identified all instances of the following types of directed male aggression (Nishida et al. 2010): (1) display, charging; (2) display, past; (3) chase; and (4) attack. We limited our analyses to those instances in which there was an unambiguous male target. We further classified each instance of directed male aggression as “solo” (a single male actor), or “coalitionary” (two to three males simultaneously directing aggression at one or more males) (Harcourt and de Waal 1992). We scored a coalition of three males (e.g., males A, B, and C) as three dyadic coalitions (A–B, A–C, B–C). We excluded events involving more than three aggressors, as these are challenging to document and analyze. In many cases, the observers were unable to determine the identity (and roles) of all participants (i.e., often the aggressors included “others”). There were only ten instances when more than three male aggressors were specifically named and it seemed that no other males were involved. Additionally, different factors are likely to affect participation in “gang” attacks versus dyadic or triadic coalitions. For these reasons, we chose to concentrate upon the clearest cases of coalitionary aggression.

Using MatMan (version 1.1, Noldus Information Technology, Wageningen, The Netherlands) and the improved

linearity test (de Vries 1995), we calculated annual male dominance ranks using pant–grunt data extracted from the narrative notes. Pant–grunts are conspicuous, submissive vocalizations that function as formal indicators of dominance (Goodall 1986). We found significant linearity ( $P < 0.05$ ) for 10 of the 14 years of the study using pant–grunts alone and a trend towards linearity ( $P < 0.1$ ) in 1 year. For the 3 years in which there was no evidence of linearity based on pant–grunt data alone, we repeated the analysis including the outcome of dyadic agonistic interactions that had an unambiguous winner and loser. This resulted in significant linearity for 1 year ( $P < 0.05$ ) and a trend towards linearity for the other 2 years ( $P < 0.1$ ). Then, based on these ranks, we classified males into yearly rank categories. The three highest-ranking males received over 75 % of all pant grunts given by males each year. Most males below this threshold received very few pant–grunts. Therefore, we created three rank categories: Alpha (highest ranking), High (second- and third-highest ranking), and Low (ranks four and below).

#### Genetic data

Since 2000, we have collected fecal samples in RNAlater (Ambion, Austin, Texas, USA). We used DNA extracted from those samples to PCR genotype each individual and determine fathers of 25 offspring that lived until at least age one. Twenty paternities are reported in Wroblewski et al. (2009). In summary, all habituated candidate males, known mothers, and offspring were PCR genotyped at minimum of 10 of 11 microsatellite loci using DNA extracted from feces preserved in RNAlater (Wroblewski et al. 2009). For those individuals, the chimpanzee-specific DNA concentration was quantified before performing genotyping from at least two independent fecal samples whenever possible. Paternity was then first examined through exclusion and confirmed using the likelihood-based paternity-assignment program CERVUS 2.0 (Marshall et al. 1998) under three simulation conditions: (A) within-community candidate males only; (B) all habituated candidate males for both the Kasekela (study community) and Mitumba (adjacent) communities; and (C) all chimpanzees alive at the time of conception for both the Kasekela and Mitumba communities and an additional 50 % unsampled male candidates to account for potential candidates from the non-habituated Kalande (adjacent) community.

For this study, we newly determined five paternities (Table S2) using essentially the same methods with minor differences. New genotypes for the Kalande community males and the 5 new offspring, as well as their corresponding paternities, were determined through the following slightly modified methods: (A) Individuals were genotyped at 8 microsatellite loci, with only one offspring (ZIN) typed at four loci (minimum: D18S536, D4S243, D10S676, D9S922; additional: D2S1326, D2S1333, D4S1627, D9S905). With

the high degree of heterozygosity (range, 0.529–1, where 1 indicates all individuals are heterozygous at that locus) and allelic polymorphism (average, seven alleles per locus) for those loci, 4–11 loci were more than sufficient to generate unique genotypes for all individuals and resolve paternity down to a single male. As with the previously determined paternities, to be identified as a father, a male had to be the only one to lack allelic mismatches with the offspring given the known mother's genotype and have 95 % confidence assigned by the most recent version of CERVUS (3.0) (Kalinowski et al. 2007). (B) Chimpanzee-specific DNA concentrations within the DNA extracts were not quantified; however, genotypes were still determined from at least two fecal sample extractions. (C) To reduce redundancy, we determined paternity in CERVUS consolidating from three to two different simulation parameters for the genotype frequencies and proportion of candidate males alive and sampled at the time of each conception: (1) strictly within-community candidate males; (2) all candidate males for both the habituated Kasekela and Mitumba communities, any genotyped males (regardless of age) opportunistically sampled from the non-habituated Kalande community, and an additional 50 % unsampled male candidates to account for potentially missed candidates from Kalande.

#### Social network analysis

For each male in each 2-year period, we used UCInet software (Borgatti et al. 2002) to calculate our four measures of network centrality: degree, strength (based on the number of coalitions per 100 h each dyad spent together), betweenness and eigenvector centrality. We normalized each network centrality measure by expressing an individual's score as a percentage relative to the maximum possible score. We determined whether the coalition networks differed from random by comparing their properties to those of corresponding random networks (Croft et al. 2008). For fully connected networks (i.e., each male was indirectly connected to all other males,  $n=5$  of 7 networks), we calculated mean shortest path length and mean clustering coefficient. We compared these parameters using two-tailed Monte Carlo tests to those of 100 random networks with the same number of nodes and ties. For networks that were not fully connected ( $n=2$ ), we compared only their mean clustering coefficients to those of random networks as mean shortest path length cannot be calculated for non-fully connected networks. All networks differed significantly from random ( $p \leq 0.05$ ).

#### Statistical analyses

We conducted two sets of regressions in SAS 9.2 (SAS Institute, Cary, North Carolina), using the Generalized

Estimating Equation (GEE) method (PROC GENMOD) to control for repeated sampling of the same males (Diggle et al. 2002). This method adjusts estimated parameter variance based on sampling frequency, and is equivalent to incorporating male ID as a random effect in a Generalized Linear Mixed Model. Prior to regressions, we tested for collinearity among all predictor variables using bivariate Pearson correlations. We considered pairs of variables to be highly collinear if the  $r$  value was greater than 0.7 (Tabachnick and Fidell 2007), however this was never the case.

In the first set of regressions, we tested whether coalitionary strength in one period increased the probability that a male would be higher ranking in the next period (Yes/No; that is, whether a given male rose either from High to Alpha, Low to High or Low to Alpha). We excluded alpha males because by definition they cannot improve their rank. However, we included coalitions involving the alpha in calculations of social network metrics for other males. Then, because high-ranking males have fewer options for hierarchy advancement than low-ranking males, we also included dominance rank (the highest yearly categorical rank a male achieved during a given 2-year period) as a main effect. We also included age (Young: 12–19 years old; Prime: 20–29 years old; Past-prime:  $\geq 30$  years old) as a factor since older males may not be able to compete as effectively as younger males. Finally, as individuals with high rates of solo aggression are expected to be more likely to experience a rank increase, we also included solo aggression rate (number of solo aggression events directed at other males per 100 h). We followed a sequential backwards elimination procedure to remove terms that did not contribute significantly ( $\alpha = 0.05$ ) to the model. We repeated this procedure for each of the other three coalition metrics, degree, eigenvector centrality, and betweenness. There were 49 data points in each of these regressions, as some males were sampled in multiple periods. For example, male FD contributed 5 data points while FE contributed one. As described above, we included male ID as a repeated measure in each model in order to control for repeated observations on the same subject.

In the second set of regressions, we tested whether coalitionary behavior in one period was positively associated with the probability of siring offspring (Yes/No) in the same period. While coalitions could theoretically increase an alpha male's reproductive success, the low variance between alpha male chimpanzees in the number of offspring sired (typically at least 1 during their tenure: Wroblewski et al. 2009) makes it difficult to quantify the effect of coalitionary aggression by alphas in this species. Therefore, we chose to focus upon the fitness benefits of coalitions for non-alpha males, for whom there is greater variation in reproductive success. In addition, it was important to use the same sample of males as in the first analysis so as not to introduce additional sources of variation. As above, we conducted

four multiple logistic regressions, one for each of the coalition metrics (degree, strength, eigenvector centrality, and betweenness), again controlling for dominance rank, age, and solo aggression rate. Additionally, we also controlled for the total number of offspring sired (by all males) during a given period to account for the fact that the probability of any male conceiving increases with the total number of offspring sired during a given period. These regressions each contained 63 data points, as the response variable did not require data from the subsequent period as it did in the previous analysis.

## Results

### Coalitions and dominance rank

We identified 365 dyadic coalitions (167 two-male and 66 three-male coalitions) among 16 males between 1995 and 2008 (Table S1). Over the course of the study, there were 14 rank increases, with 10 ascensions from Low to High, 1 from Low to Alpha, and 3 from High to Alpha (Table S1). Neither coalitionary network degree, strength, nor eigenvector centrality was associated with rank increase (Table S3a, b, c). However, there was a statistically significant association between coalition network betweenness and the probability of achieving higher dominance rank in the subsequent period (Table 1). To illustrate this result graphically with an example, Fig. 2a depicts the coalition network in 1997–1998. Here, the two males with the highest betweenness (AO and WL) were the only males to have higher ranks in the next period—both ascending from low- to high ranking. All variables contributed significantly to the model fit. As expected, males who directed the greatest rate of solo aggression at other males were most likely to increase in rank, while past-prime and high-ranking males were least likely to do so (Table 1). Sociograms from all periods are displayed in Fig. S1.

### Coalitions and reproductive success

Next, we asked whether coalitionary behavior increased the chances of siring offspring within a given 2-year period. Neither coalition network degree, strength, nor eigenvector centrality was associated with an increased probability of paternity (Table S4a, b, c). However, once again, there was a significant positive association between coalition network betweenness and the probability of siring at least one offspring within the same 2-year period (Table 2). For example, the only non-alpha males to sire offspring in 1997–1998 were WL and KS, who had the highest betweenness scores (Fig. 2a). Similarly, in 2007–2008, (Fig. 2b), the only non-alpha male to sire offspring (SL) had the highest betweenness of any

**Table 1** Results of multivariate logistic regression for the effect of coalition network betweenness on probability of increasing in rank

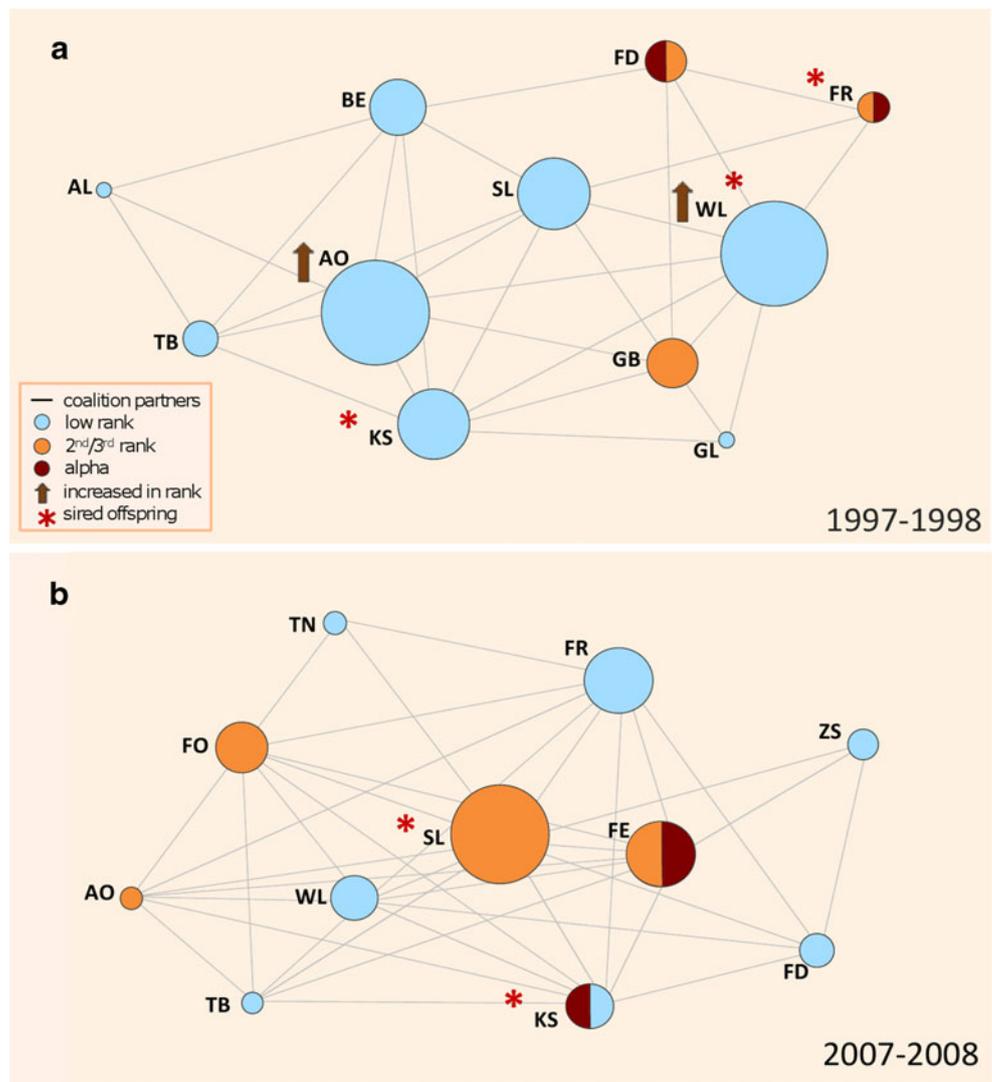
Variable	Comparison	Estimate	X <sup>2</sup>	p value
Intercept		-1.52	6.40	0.01
Coalition Network Centrality (Betweenness)		8.11	3.69	0.045
Dominance rank	High vs. low	-3.32	3.92	0.047
Age	Past-prime vs. young	-2.34	11.97	0.0005
	Past-prime vs. prime	-1.88	2.79	0.095
	Prime vs. young	-0.46	1.32	0.248
Solo aggression rate		1.67	7.62	0.006

Values in italics indicate statistical significance ( $\alpha=0.05$ ). All variables in the initial model were significant predictors of our dependent variable. With all other factors controlled for, a male's coalition network betweenness in one 2-year period was positively associated with the probability of being higher ranking in the next. All else equal, males with high rates of solo aggression had a higher likelihood of becoming higher ranking than less aggressive males. Past-prime, high-ranking males were least likely to increase in rank.  $N=13$  males, 49 data points (Table S1)

male. (KS sired one offspring while he was still alpha male in early 2007). We removed age and solo aggression rate from the model as they had no effect on the

probability of siring offspring. Notably, high-ranking non-alpha males were less likely to sire offspring than low-ranking individuals (Table 2).

**Fig. 2** Representative coalition networks. Each node represents a male. A line connecting two nodes indicates that these males formed a coalition at least once during that 2-year period. Node diameter is proportional to betweenness and color depicts dominance rank (maroon Alpha, orange High, blue Low). A bi-colored node indicates that a change of alpha male occurred within that 2-year period; the left side represents that male's rank at the start of the period. Asterisks identify males who sired offspring within that period; "up" arrows identify males who were higher ranking in the next period. Males with high betweenness sired offspring within that 2-year period (a, b) and/or became higher ranking in the next period (a) (note: b represents the final study period and thus ranks of these males in the 2 years that followed are unknown). FR became alpha male in September 1997, and the offspring he fathered was sired after this date. KS sired an offspring before he lost the alpha position in March 2008. Networks were created using the spring-embedding algorithm in NetDraw (Borgatti 2002).



**Table 2** Results of multivariate logistic regression for the effect of coalition network betweenness on probability of paternity

Variable	Removal order	Comparison	Estimate	$\chi^2$	<i>p</i> value
Intercept			–2.83	19.45	<0.0001
Coalition Network Centrality (Betweenness)			9.00	4.41	0.036
Total conceptions			0.37	8.94	0.003
Dominance Rank		High vs. Low	–2.13	4.88	0.027
Solo aggression rate	1		–0.53	0.69	0.41
Age	2	Past-prime vs. young	–0.13	0.02	0.88
		Past-prime vs. prime	–0.61	0.47	0.49
		Prime vs. young	–0.74	1.12	0.29

Values in italics indicate statistical significance ( $\alpha=0.05$ ). Solo aggression rate and age were sequentially removed as they did not contribute significantly to the model fit. All else equal, a male's betweenness in the coalition network for a given period was positively associated with the probability of siring offspring within that same period. High-ranking (non-alpha) males were significantly less likely than low-ranking males to sire offspring.  $N=16$  males, 63 data points (Table S1)

## Discussion

We have shown that coalitionary aggression among male chimpanzees in Gombe National Park is associated with long- and short-term fitness benefits. First, males with high centrality in the coalition network were more likely to increase in rank. While our results show that being high-ranking may be temporarily disadvantageous with regard to securing short-term paternity (consistent with genetic data from Gombe showing that high-ranking males have lower reproductive success than expected (Wroblewski et al. 2009)), three of the four males who became alpha ascended from a high-ranking position. Since the alpha male has the highest probability of siring offspring (Wroblewski et al. 2009), becoming high-ranking appears to be a tactic that leads to fitness payoffs. Second, males with high centrality were more likely to sire offspring in a given period than other males of similar rank. In addition to demonstrating that coalitionary aggression increases reproductive success in this species, this study highlights the importance of social connections in determining fitness, independently of dominance rank.

In particular, we found that males that benefited from coalitions were those with high betweenness, based on their tendency to form coalitions with individuals who did not form coalitions with each other (Girvan and Newman 2002, Lusseau and Newman 2004). Maximizing betweenness is an efficient way of achieving high connectivity in a network because it does not require forming coalitions with everyone. Instead, it depends upon having the “right” social connections, an idea which emerged before social network analyses became popular in behavioral ecology (e.g., Noë 1992). A potential proximate explanation of how high betweenness in the coalition network could lead to high rank and to the production of offspring is that to avoid jeopardizing long-term relationships, males may refrain from

forming coalitions against those with whom they share many partners (Girvan and Newman 2002). For example, in 1997–1998 (Fig. 2a), AO did not form coalitions with the two highest-ranking males, FD and FR. However, many of AO's direct partners (e.g. BE, SL, GB) did form coalitions with these high-ranking males. If FD and FR avoided forming coalitions against individuals with whom they shared several partners, they would have infrequently targeted AO, a factor which may have been crucial to his subsequent increase in rank. In contrast, a male such as AL, who shared only one partner (BE) with FD and none with FR, may have been a more likely target of these two males. Interestingly, examining in detail the relationships between these four males in this 2 year period revealed that, in fact, this was not the pattern that emerged. Three of FD's nine coalitions during this period were directed at AO, compared to only one against AL. FR formed a coalition against AO once, but never targeted AL. As our analyses have revealed, several factors combine to affect hierarchy ascension and paternity, including age and rank. Clearly, more detailed data are needed to fully understand this complicated system.

It is unlikely, given the small number of coalition metrics examined (4), that betweenness emerged as a significant predictor of both dependent variables (reproductive output and the likelihood that males would rise in dominance rank) by chance. However, we cannot rule out the possibility that coalitionary betweenness arises as an emergent property of another facet of the social network. For example, males may not be cognizant of others' coalition partners, but instead, the decision to form a coalition is based on the identity of the target. In this case, the rival's association preferences would dictate a male's position in the coalition network. Alternatively, the correlation between fitness and betweenness may arise as a byproduct of other traits that increase the probability of increasing in rank and/or reproducing. Testing these possibilities will require identification of the males

responsible for initiating coalitions and soliciting aid. Additionally, close examination of affiliative (e.g., grooming) partners, which are important predictors of fitness in other primates (Silk et al. 2010), may also shed light on the association between coalitionary aggression and fitness. For example, it may be the structure of social bonds that generates the observed properties of the coalition network.

Our data indicate that male coalitionary aggression at Gombe is relatively rare. This is undoubtedly due in part to the fact that we have concentrated upon instances of aggression with sufficient detail to classify as coalitionary or solo. As a point of comparison, during 2 years of intensive observation of adult males in a community of comparable size (Kanyawara, Kibale National Park, Uganda), Duffy et al. (2007) observed 58 coalitions involving the alpha male. In our study, alpha male KS participated in 31 coalitions between 2005 and 2006. While as many as 32 coalitions per month have been observed at Ngogo (Kibale National Park, Uganda) (Mitani et al. 2002), these data come from a community with more than twice as many adult males than at Gombe and from targeted follows of parties with many adult males. During 390 h of observation of M-Group (nine males) at Mahale Mountains National Park, Tanzania, Nishida and Hosaka (1996) observed a total of 40 coalitions (7 “communal attacks”, 11 “actor-alliances” and 22 “reactor-alliances”). During 367 h of observation at Taï National Park, Côte d’Ivoire (ten males), Boesch and Boesch-Achermann (2000) recorded 30 “supporting coalitions” and 19 “joint attacks”. Several of these involved more than two aggressors and/or a female target. To our knowledge, studies of male aggression and social bonding at Gombe (e.g., Goodall 1986, Bygott 1979) and Budongo Forest, Uganda (e.g., Newton-Fisher 1999, 2002) have not reported coalition rates. While our use of long-term data may have limited our sample, it enabled us to examine a longer time frame, and consequently address a question that cannot be answered with short-term data—that is, whether coalitionary aggression had fitness consequences in subsequent years.

As a result, our study is the first to demonstrate a clear link between fitness and coalitionary behavior in this species. Nevertheless, we cannot address the direction of causation with these data. For example, it is possible that an increase in rank leads to more (or different) coalitionary behavior. However, whichever direction the causal arrow points, our data support the notion that effective navigation of the social landscape is crucial for many group-living animals and may be a driving force behind the evolution of brain size (Dunbar and Shultz 2007). Although the ability to recognize the relationships of others (Cheney and Seyfarth 2007) is a critical component of social intelligence, how animals use this information and whether or not it impacts upon their fitness is largely unknown (Cheney

2011). In addition to confirming the long-held assumption that coalitionary aggression increases reproductive success, our data suggest there are fitness consequences to the recognition of third-party relationships. As such, it represents an important step toward a more complete understanding of the adaptive value of social intelligence and the evolution of cooperation.

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