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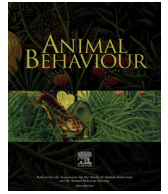
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Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba



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Patterns of coalitionary aggression among female animals are generally explained by kin selection theory. Frequent female coalitions are almost exclusively observed in female-philopatric species, where females stay in their natal group, and females typically form coalitions with their kin. Bonobos, *Pan paniscus*, in contrast, are male-philopatric, with females emigrating to new groups at adolescence, but female bonobos frequently form coalitions even though they are generally with nonrelatives. Here we investigated the patterns of female coalitions in a group of wild bonobos at Wamba, Democratic Republic of the Congo, in order to explore alternative mechanisms to kin selection for cooperation among females. We found that all female coalitions (defined as coalitions in which two or more females participated) were formed to attack males, usually after the male(s) behaved aggressively towards one or more females. There was no evidence that female bonobos used proximity, grooming or genito-genital rubbing (GG-rubbing) to develop coalition partnerships, although higher association provided females with more opportunity to form coalitions. Instead of reciprocal agonistic support, we found a unidirectional pattern in which older females supported younger females. Females defeated males more easily when they formed coalitions than when they confronted males alone. Unlike female coalitions in other species that use coalitions to cope with competition among females, our results suggest that coalitions in female bonobos might have evolved as a counterstrategy against male harassment. Females might choose their coalition partners based not on affiliative relationship or reciprocity but on mutualism. In contrast to the hypothesis that affiliative behaviour leads to coalition formation, coalitions might in fact increase gregariousness among females, leading females to develop affiliative interactions that promote tolerance. © 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Cooperation is widespread in the animal kingdom, ranging from cooperative breeding (Clutton-Brock, 2002; Wong & Balshine, 2011) to food sharing (Carter & Wilkinson, 2013), allogrooming (Pettis & Pankiw, 1998; Schino & Aureli, 2008) and coalitionary aggression. Coalitionary aggression, hereafter referred to as 'coalition(s)', involves two or more individuals cooperating to attack a common conspecific target (Bisonnette et al., 2015; Harcourt & de Waal, 1992), and is observed in species that exhibit complex in-group social relationships. The choice of coalition partner is typically not random (reviewed in Smith et al., 2010); rather, patterns of intragroup coalition formation are explained by kin selection (Hamilton, 1964; Silk, 2002), reciprocity (Trivers, 1971) and mutualism (Bercovitch, 1988; West-Eberhard, 1975). Previous studies on primates (reviewed in Kapsalis, 2004; Silk, 2002, 2006; Sterck,

Watts, & van Schaik, 1997) and other social animals (reviewed in Smith, 2014; Smith et al., 2010) have revealed that the general pattern of coalition formation among females is well explained by kin selection theory. Female–female coalitions are observed almost exclusively in female-philopatric species, where females stay within their natal groups, and primarily among close kin (Silk, 2006; Smith et al., 2010; Sterck et al., 1997). Female affiliative interactions and coalition formation are largely biased towards kin and are stable for long periods. Such a long-term relationship, characterized by repeated coalition formation and high levels of affiliation, is called an 'alliance' (Bisonnette et al., 2015).

In evolutionary models, alliances among kin are among the most important factors shaping female social relationships in primates (van Hooff & van Schaik, 1992; van Schaik, 1989; Sterck et al., 1997; Wrangham, 1980). In a highly competitive environment, related females should benefit from supporting each other to protect resources, thereby creating selective pressure for staying with kin and, eventually, evolving a female-philopatric, nepotistic society. In situations with low competition, without selective pressure to

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support kin, females are more likely to disperse and their society will be non-nepotistic. This model successfully explains why frequent female coalitions are observed almost exclusively in female-philopatric species, and why females form alliances with their kin. However, there is a striking exception that does not fit the model: female bonobos, *Pan paniscus*, form coalitions frequently (Parish, 1996; Stevens, Vervaecke, de Vries, & van Elsacker, 2006; Surbeck & Hohmann, 2013) even though the coalitions are generally between nonrelatives due to the pattern of female dispersal (Eriksson et al., 2006; Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999; Hashimoto, Takenaka, & Furuichi, 1996; Kano, 1992; Sakamaki et al., 2015). If the kin selection model, which explains female coalitions so well in other species, cannot explain coalitions for female bonobos, then why and how do female bonobos form coalitions? Bonobos provide a valuable opportunity to understand the mechanism of cooperation among females without direct kin selection.

Chimpanzees, *Pan troglodytes*, and bonobos are very closely related. Both live in multimale/multifemale groups and have a fission–fusion social system in which a group splits into temporary subgroups (called ‘parties’; Nishida, 1968; Kano, 1982, 1992). Additionally, both species have a strong female-biased dispersal pattern (Eriksson et al., 2006; Goodall, 1986; Kano, 1982, 1992; Nishida, 1979; Sakamaki et al., 2015), although the tendency of female dispersal may be stronger in bonobos; female chimpanzees occasionally stay in their natal group (Foerster et al., 2015; Goodall, 1986; Nakamura, 2015), and such a case has not yet been reported in bonobos. Despite these similarities in basic social structure, chimpanzees and bonobos show a considerable difference in their patterns of coalition formation.

Social bonds in female chimpanzees are known to be weak, although there is interpopulation variation in female sociality (Lehmann & Boesch, 2008). Females tend to range alone with their offspring except during oestrus, and they seldom engage in affiliative interactions in Gombe (Foerster et al., 2015; Goodall, 1986), Mahale (Hasegawa, 1990; Nishida, 1979), Kanyawara (Otali & Gilchrist, 2005; Pepper, Mitani, & Watts, 1999) and Kalinzu forest (Hashimoto & Furuichi, 2015). Females in Tai forest (Boesch & Boesch-Achermann, 2000), Ngogo (Wakefield, 2008) and Sonso (Emery-Thompson & Wrangham, 2006) are relatively more gregarious than females in other field sites, but average female–female associations and affiliative interactions are still less frequent than those of males (Tai forest, Lehmann & Boesch, 2008; Ngogo, Langergraber, Mitani, & Vigilant, 2009; Sonso, Arnold & Whiten, 2003). Female coalitions are rare (Newton-Fisher, 2006), but have been reported at some field sites where females are more gregarious (Tai forest and Sonso, Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2006) and also in captivity (Baker & Smuts, 1994; de Waal, 1984).

Male chimpanzees engage in strong, durable affiliative relationships and frequently form coalitions (Boesch & Boesch-Achermann, 2000; Mitani, 2009; Nishida & Hosaka, 1996). Forming coalitions provides chimpanzee males with direct fitness benefits such as rank improvement and increased number of offspring (Gilby et al., 2013). Early research explained their coalitions by kin selection (Goodall, 1986), and later empirical studies showed that they form coalitions with both close and distant relatives when they are able to gain benefits from the coalition (Langergraber, Mitani, & Vigilant, 2007; Mitani, Merriwether, & Zhang, 2000). Although the formation of coalitions is often temporary and flexible (Boesch & Boesch-Achermann, 2000; de Waal, 1982, 1984), males choose coalition partners based on their daily social relationships and reciprocity. Males who are more frequently associated spatially and who groom each other are more likely to form coalitions (Hemelrijk & Ek, 1991; Nishida, 1983; Watts, 2002), and they

support each other reciprocally (Mitani, 2006; de Waal & Brosnan, 2006; Watts, 2002). Some male dyads form alliances, which can sometimes last for years (Gilby & Wrangham, 2008; Mitani, 2009; Nishida, 1983; Nishida & Hosaka, 1996; de Waal, 1982; Watts, 2002).

In wild bonobos, affiliative relationships among males are weaker than in male chimpanzees, and male bonobos seldom form coalitions (Furuichi & Ihobe, 1994; Ihobe, 1992; Surbeck & Hohmann, 2013). Female bonobos, on the other hand, are much more social than female chimpanzees and tend to range in large mixed-sex parties, keeping close association with other individuals (Furuichi, 2009, 2011; Hohmann & Fruth, 2002; Kano, 1992; Kuroda, 1979; White, 1988, 1998). Grooming interactions among female bonobos are as frequent or more frequent than among males or between unrelated males and females (Furuichi, 1997; Furuichi & Ihobe, 1994; Stevens et al., 2006). Moreover, females form coalitions more frequently than do males (Stevens et al., 2006; Surbeck & Hohmann, 2013).

The social status of female bonobos is equal to or higher than that of males, and females have feeding priority (Furuichi, 1997, 2011; Surbeck & Hohmann, 2013; White & Wood, 2007). Female rank and social centrality is thought to be acquired and maintained by female aggregation and coalitions (Furuichi, 2011; Parish, 1994, 1996; Parish & de Waal, 2000; Vervaecke, Vries, & Elsacker, 1999; White & Wood, 2007). Researchers have proposed that affiliative interactions among female bonobos, especially genito-genital or ‘GG’-rubbing (Kuroda, 1980), have evolved to promote coalition formation (Parish, 1996). However, one study on wild bonobos at Lui Kotale did not find a tendency for females to choose close associates or GG-rubbing partners as coalition partners (Surbeck & Hohmann, 2013).

In this way, female coalitions have been considered paramount for shaping the social lives of bonobos. Despite their apparent importance, there have been few systematic studies on coalition formation in bonobos (Stevens, Vervaecke, de Vries, & van Elsacker, 2007). Do female bonobos form coalitions based on their affiliative relationships and reciprocity, as male chimpanzees do? The aim of this study was to clarify the pattern of coalition formation and investigate the factors that promote coalition formation among wild female bonobos. We first investigated the size, target and context of female coalitions. We then examined whether daily affiliative relationships promote coalition formation and whether agonistic support is reciprocal. Additionally, we examined the potential risks and benefits for female bonobos of forming coalitions.

METHODS

Study Site and Subjects

Observations were conducted on wild bonobos, in the PE group, at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, where long-term research has been conducted since 1974 (Kano, 1992). From 1976, researchers were aware of the presence of bonobos in PE group’s current range, and at the time they named them ‘P group’ (Idani, 1990; Kano, 1982; Kuroda, 1979). Research at Wamba was disrupted from 1996 because of political instability and restarted in 2003 with continuous daily observation of P group’s neighbouring group, E1 group. In September 2010, we started habituation and daily following of a group of bonobos in P group’s old range, and named them ‘PE group’. PE group and P group are probably the same because two parous females from P group are present in PE group.

At the time of the present study, PE group consisted of 26–27 individuals. All individuals were identified and habituated from the beginning of the study period. Our study subjects were individuals

who were more than 8 years old, but we excluded one female who emigrated during the study period (15 individuals: nine females and six males, Table 1). Data on females who temporarily visited this group were not analysed. We estimated the age of individuals based on their physical features. Individuals estimated to be 35 years old or more were classified as old, and individuals from 21 to 34 years old were classified as middle-aged. Individuals less than 21 years old were classified as young. We could not confirm the linear dominance relationship for females because aggressive interactions among them were very rare (28 dyadic aggressive interactions among only 12 of 36 female–female dyads). However, social rank and age are strongly correlated in wild female bonobos in that older females are higher ranking than younger ones (Furuichi, 1989, 1997), and all of our female–female dyadic aggression data also followed this tendency.

Behavioural Observation

Bonobos were followed for a total of 1889 h by author N.T. with two local assistants from June to November 2012, August 2013 to January 2014, July to September 2014 and January to June 2015. When bonobos split into several parties, the largest party was followed. We recorded all observed intragroup aggressive interactions, which, by definition, included at least one aggressive behaviour. Aggressive behaviours were as follows: vocal or nonvocal threatening, directed displaying, charging, chasing and physical attack (kick, beat, grabbing, etc.). Submissive behaviours were as follows: avoiding, jumping aside, fleeing, grimacing and screaming. When at least one submissive behaviour was observed, we judged that the submissive individual had lost the aggressive interaction. When both individuals grimaced or screamed, the individual who fled from the opponent was considered the loser. There were no cases where both individuals grimaced or screamed and neither of them fled. If two or more individuals jointly attacked one or more common target(s), we recorded the attack as a coalition (Harcourt & de Waal, 1992). Coalitions in which two or more females participated were termed ‘female coalitions’. We recorded the direction of agonistic support only when we could clearly identify the supporter(s) and receiver(s). Frequency of coalition formation of a dyad (A & B) was calculated as follows (Cairns & Schewager, 1987):

$$Co(ab)/(Ag(a) + Ag(b) - Ag(ab))$$

Co(ab) = number of coalitions A and B formed with each other
 Ag(a) = number of aggressive interactions in which A participated
 Ag(b) = number of aggressive interactions in which B participated

Ag(ab) = number of aggressive interactions in which A and B both participated

The affiliative relationship of each female–female dyad was evaluated using four measures: frequency of (1) attendance in the same party, (2) spatial proximity, (3) grooming interactions and (4) GG-rubbing. We recorded party composition every 60 min: the IDs of bonobos in sight at the beginning of each hour and new individuals as they appeared until the end of the hour (1 h party method: Hashimoto, Furuichi, & Tashiro, 2001; Mulavwa et al., 2008). We also recorded grooming interactions and spatial proximity by instantaneous scan sampling (Altmann, 1974) at 5 min intervals and, for all visible individuals, we recorded whether they were in close proximity (less than 3 m) or grooming with any other individuals, although proximity was not recorded when the general behaviour of the party was travelling because of the difficulty of recording precise data. We collected 5079 ± 1253 scan samples per subject female (average ± SD). GG-rubbing was observed ad libitum (Altmann, 1974). For each measure, we calculated the strength of a dyad (A & B) as follows (Cairns & Schewager, 1987):

- (1) same-party attendance index (ab) = Pa(ab)/(Pa(a) + Pa(a) – Pa(ab))
 Pa(ab) = number of 1 h party segments in which both A and B were observed
 Pa(a) = number of 1 h party segments in which A was observed
 Pa(b) = number of 1 h party segments in which B was observed
- (2) proximity index (ab) = Pr(ab)/Sc(ab)
 Pr(ab) = number of scans in which A and B were within 3 m of one another
 Sc(ab) = number of scans containing both A and B
- (3) grooming index (ab) = Gr(ab)/Sc(ab)
 Gr(ab) = number of scans in which A and B engaged in grooming interactions
- (4) GG-rubbing index = GG(ab)/Pa(ab)
 GG(ab) = number of GG-rubbing events between A and B

Data Analysis

We used R 3.1.2 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) for all statistics except for analysis of reciprocity of agonistic support, in which case we used MATSQURE (Hemelrijk, 1990).

We ran a generalized linear mixed model (GLMM, package ‘lme4’; Douglas, Martin, & Ben, 2012) to assess the relationship

Table 1
 Study subjects, estimated age, age category and their dependent offspring

Name (abbreviation)	Sex	Estimated age in 2012	Age class	Dependent offspring (born year)
Bokuta (Bk)	Female	49	Old	–
Kabo (Kb)	Female	39	Old	♀(2006), ♂(2012)
Hide (Hd)	Female	35	Old	♀(2006), ♂(2011)
Maluta (Mt)	Female	27	Middle	♂(2006), ♀(2012)
Pao (Po)	Female	21	Middle	♀(2009), ♀(2013)
Ichi (Ic)	Female	21	Middle	♀(2007), ♂(2012), ♀(2015)
Saku (Sk)	Female	17	Young	♀(2009), ♀(2013)
Marie (Mr)	Female	12	Young	♀(2014)
Nara (Nr)	Female	11	Young	♀(2014)
Gai (Gl)	Male	39	Old	
Malusu (ML)	Male	30	Middle	
Turkey (TK)	Male	21	Middle	
Snare (SN)	Male	20	Middle	
Daniel (DN)	Male	17	Young	
Ikura (IR)	Male	8	Young	

between sex combinations and frequency of coalition formation, using the coalition frequency as the dependent variable, using the 'cbind function' and the error distribution 'binomial'. We entered the sex combination of each dyad as a fixed factor. Identity of the individuals in the dyad were used as random effects to take into account individual differences. We ran a series of GLMMs to assess the relationship between a female's affiliative relationships and frequency of coalition formation. We used the frequency of coalition formation of female dyads as the dependent variable, using the 'cbind function' and the error distribution 'binomial'. We entered the same-party attendance index, proximity index, grooming index and GG-rubbing index of each female dyad as a fixed factor in each model. The identities of the individuals in the dyads were entered as random effects. Prior to the analysis, we checked the distribution of the predictors and square-root-transformed 'grooming index' and 'GG-rubbing index' to achieve approximate normality.

A Kr matrix correlation test was used to examine reciprocity of given and received agonistic support using Hemelrijk's MATSQURE (Hemelrijk, 1990). This test analyses group level reciprocity by calculating the correlation between a supporter–receiver matrix and its inverse.

Ethical Note

Our study was approved by the Ministry of Scientific Research, Democratic Republic of the Congo, and conformed to the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University. Our investigation followed the International Primatological Society guidelines for the study of nonhuman primates.

RESULTS

Sex Combination of Dyads and Frequency of Coalition Formation

We observed 699 separate aggressive interactions (403 male–male, 28 female–female and 268 intersex) and 108 coalitions: 58 coalitions were formed only by females, nine only by males and 41 by female(s) and male(s). Coalitions were significantly more frequent in female–female dyads than in male–male or intersexual dyads (GLMM: number of pairs = 105, Table 2: Model 1, Fig. 1).

Table 2
Results of GLMMs

Predictor variables	Estimates	SE	Z	P
Model 1				
Intercept	−3.73	0.36	−10.28	<0.01
Sex				
F–F vs F–M	−1.82	0.44	−4.14	<0.01
F–F vs M–M	−1.72	0.60	−2.86	<0.01
Model 2				
Intercept	−0.69	1.23	−5.6	<0.01
Same party attendance index	6.31	2.07	3.05	<0.01
Model 3				
Intercept	−3.31	0.32	−10.26	<0.01
Proximity index	0.47	1.44	0.32	0.75
Model 4				
Intercept	−3.31	0.31	−10.63	<0.01
Grooming index	0.42	1.13	0.37	0.71
Model 5				
Intercept	−3.48	0.37	−9.41	<0.01
GG-rubbing index	2.50	2.94	0.84	0.40

The frequency of forming coalitions in relation to sex combination (Model 1), same-party attendance index of the female dyads (Model 2), proximity index of the female dyads (Model 3), grooming index of the female dyad (Model 4), and GG-rubbing index of the female dyads (Model 5). Overall, both Model 1 and Model 2 were statistically significant ($P < 0.01$). F: female; M: male.

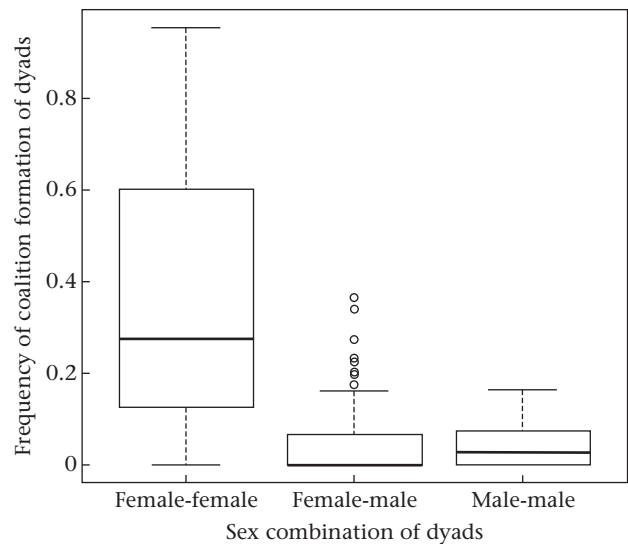


Figure 1. Sex combinations and frequency of forming coalitions. The frequency of coalition formation of each dyad was calculated as (number of coalitions A and B formed with each other) divided by (number of aggressive interactions A attended) + (number of aggressive interactions B attended) – (number of aggressive interactions A and B both attended). The boxes span the first to the third quartile and lines inside the boxes show the median. Whiskers above and below the boxes show the location of the minimum and maximum, excluding outliers which are represented by circles.

Size, Target, Severity, and Context of Female Coalitions

Two or more females took part in 73 coalitions. Of those coalitions, 15 included one or more males. Each female coalition contained 2.72 ± 0.97 individuals on average (2–6 individuals, 2.44 females and 0.28 males). All of the targets of female coalitions were male(s), of which most (95.5%) were adult. Females never formed coalitions to attack other females. Only four female coalitions (5.5%) involved just threatening, while 55 (75.3%) involved charging or chasing. Females engaged in physical attacks in 14 female coalitions (19.2%), and in one case the target male was injured, losing the tip of the second digit on his right foot.

Fifty female coalitions (68.5%) were formed during or immediately after a male's aggressive behaviour or undirected display towards or around one or more females. Nine (12.3%) were formed to aid a male during male–male aggression, and one (1.4%) was formed towards a male who was persistently soliciting copulation. The provocation was not known for another 13 coalitions.

Female–Female Affiliative Relationship and Coalition Formation

For female dyads, there was a positive correlation between same-party attendance index and frequency of coalition formation (GLMM: number of pairs = 36, Table 2: Model 2, Fig. 2a). However, proximity, grooming and GG-rubbing indices did not correlate significantly with frequency of coalition formation (GLMM: number of pairs = 36, Table 2: Models 3, 4, 5, Fig. 2b–d).

Direction and Reciprocity of Female Agonistic Support

Direction of agonistic support was known in 47 female coalitions, but nine coalitions in which females supported a male were excluded. These coalitions were divided into 54 supporter–receiver interactions. There was a significant negative relationship between support given and support received (tau Kr-test, 2000 permutations, Tau Kr = −0.38, $P = 0.026$; Fig. 3). Therefore, the agonistic support was not reciprocal. Moreover, the negative

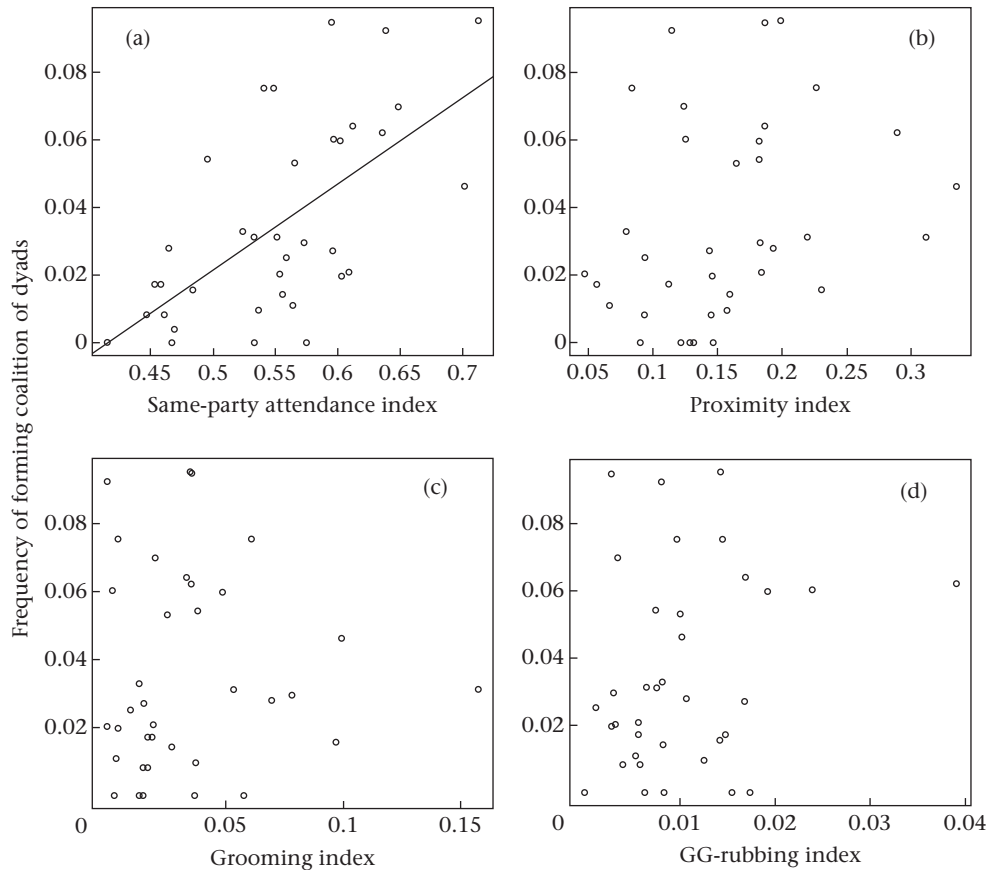


Figure 2. Affiliative relationships and the frequency of forming female–female coalitions. (a) Same-party attendance index. (b) Proximity index. (c) Grooming index. (d) GG-rubbing index. Each dot represents one female–female dyad. The frequency of coalition formation of each dyad was calculated as (number of coalitions A and B both attended in the same side) divided by (number of aggressive interactions A attended) + (number of aggressive interactions B attended) – (number of aggressive interactions A and B both attended).

correlation indicates that individuals who frequently gave support tended not to receive support and vice versa. Table 3 shows the matrix of agonistic support.

Apparently, the exchange of agonistic support between individuals within dyads was strongly biased to one side of the dyad. Forty-four instances of support (81.5%) were given across different

age categories (Table 4). In 95.5% of coalitions, older females supported younger females (binomial test: $N = 44$, $df = 1$, $P < 0.01$).

Risks and Benefits of Forming Female Coalitions

Since female coalitions were only directed towards males, we consider the results for intersex aggression here. We observed 199 dyadic intersex aggressive interactions. Of these, submissive behaviour(s) was observed in 152. Of the 152 decided dyadic intersex aggressive interactions, females won 105 (68.9%) and males won 47 (31.1%). Old females were more likely to win conflicts against males than were young females (old females: 84.0%; middle-aged females: 69.5%; young females: 29.3%; chi-square multicomparison test using Ryan’s method: a significant difference was detected only between old females and young females: $df = 2$, $P < 0.01$). When females formed coalitions, 100% ($N = 73$) won against a target male(s). We never observed a target male(s) opposing female coalitions, and females were never injured during coalition events. The winning rate was higher in any age category when females formed coalitions than when they did not (Mantel–Haenszel chi-square test: old: $\chi^2_1 = 11.55$, $P < 0.01$; middle-aged: $\chi^2_1 = 19.64$, $P < 0.01$; young: $\chi^2_1 = 21.37$, $P < 0.01$; Fig. 4).

DISCUSSION

We investigated patterns of coalition formation in female bonobos. Female bonobo social relationships are unusual in that they have strong female social bonding within a female dispersal society. In this study, female–female dyad coalitions were formed

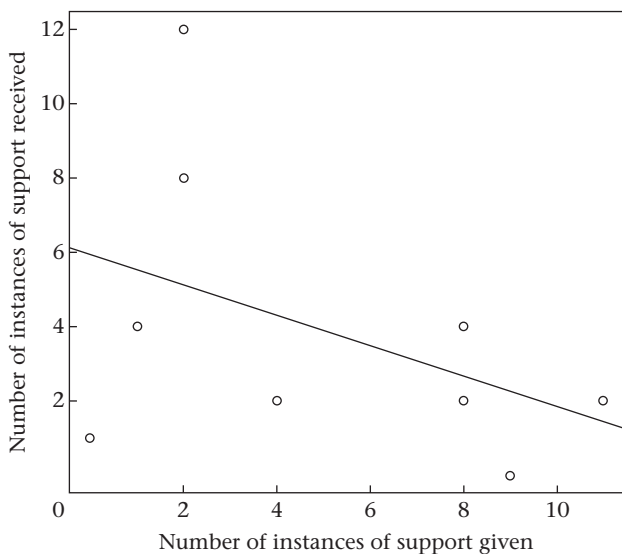


Figure 3. Number of instances of agonistic support (giving and receiving). Each dot represents an independent female.

Table 3
Matrix of agonistic support

Age category	Supporter	Recipient of support								
		Bk	Kb	Hd	Mt	Po	Ic	Sk	Mr	Nr
Old	Bk	0	2	0	1	4	1	0	0	
Old	Kb	0	0	1	2	6	0	1	0	
Old	Hd	1	0	1	2	2	7	3	0	
Middle	Mt	0	0	0	0	1	0	1	1	
Middle	Po	0	0	0	1	3	5	0	1	
Middle	Ic	0	0	0	0	0	3	0	0	
Young	Sk	1	0	0	0	0	0	2	0	
Young	Mr	0	0	0	0	0	1	0	0	
Young	Nr	0	0	0	0	0	0	0	0	

The first column gives the age category of each female.

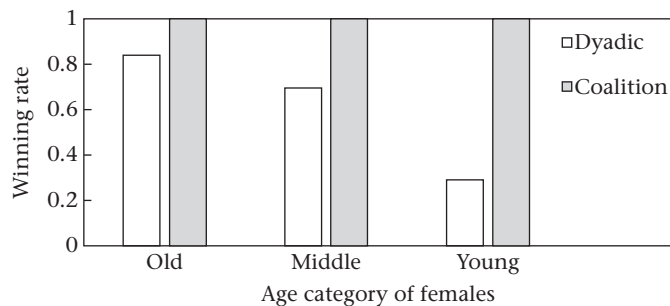
Table 4
The direction of support given across age categories

Age categories	Direction of support	
	Older supports younger	Younger supports older
Old-middle	19	0
Old-young	12	1
Middle-young	11	1
Sum	42	2

more frequently than male–male dyads and male–female dyads, as confirmed in other studies (e.g. Stevens et al., 2006; Surbeck & Hohmann, 2013).

In other species, female coalitions are generally used for female–female competition, to maintain social status or to usurp valuable food resources among females (Isbell & Young, 2002; Silk, Alberts, & Altmann, 2004; Smith et al., 2010; Sterck et al., 1997). However, in this study, female bonobo coalitions were never directed towards other females. All female coalitions were directed towards males, especially when the male was behaving aggressively towards females. Females were tolerant of each other, and aggression among females was rare. Similarly, in captive bonobos, female–female aggression seldom elicited support from other individuals (Vervaecke, de Vries, & van Elsacker, 2000b). These results suggest that female coalitions have evolved as a strategy not to cope with competition among females but, rather, to cope with intersex competition, i.e. to prevent harassment by males.

Although females of other nonhuman primates typically form coalitions with their close kin, there are episodic examples of unrelated females cooperating to attack a male (reviewed by Smuts & Smuts, 1993; see also Setchell, Knapp, & Wickings, 2006). This kind of female coalition may benefit all females by deterring all males from attacking females because of the risk of counteraggression from female coalitions (Setchell et al., 2006; Smuts & Smuts, 1993).

**Figure 4.** Females' winning rate against males in each age category. White bar: winning rate of females in dyadic aggressive interactions; grey bar: winning rate of females when they formed a coalition.

Sterck et al. (1997) did not support the hypothesis that female coalitions evolved as a strategy to counter male harassment in nonhuman primates, since establishing good relationships with males might be more effective. However, coalitions of female bonobos have been considered to be useful for preventing male harassment (Furuichi, 2011; Hohmann & Fruth, 2003; Kano, 1992; Parish, 1994, 1996; White & Wood, 2007), and our results support this view.

This does not mean that female bonobos devote less effort to establishing good relationships with males. They groom unrelated males at least as frequently as they do other females (Furuichi & Ihobe, 1994; Hohmann, Gerloff, Tautz, & Fruth, 1999; Stevens et al., 2006). Female bonobos do not suffer severe aggression from males (Furuichi, 1997, 2011; Hohmann & Fruth, 2003; Vervaecke et al., 1999) or infanticide (Wilson et al., 2014), whereas female chimpanzees do suffer from these (Feldblum et al., 2014; Hamai, Nishida, Takasaki, & Turner, 1992; Muller, Kahlenberg, & Wrangham, 2009; Wilson et al., 2014). Using both strategies, i.e. coalitions among females against males and establishing good relationships with males, female bonobos might effectively prevent harassment by males.

We found that female dyads with a higher same-party association formed coalitions more frequently. However, spatial proximity and grooming were not significantly correlated with coalition formation. Perhaps surprisingly, the frequency of GG-rubbing, which is proposed to promote female–female social bonding and coalition formation (Paoli, Tacconi, Tarli, & Palagi, 2007; Parish, 1996), did not have a significant effect on coalition formation either, corroborating findings at Lui Kotale (Surbeck & Hohmann, 2013). These results indicate that presence in the same party is more important for coalition formation than specific affiliative behaviours.

Even though females did not choose their close 'friends' as coalition partners, affiliative interactions might enhance female coalitions. Affiliative interactions may be exchanged for tolerance. Grooming is exchanged for tolerance during feeding in several primate species (rhesus macaques, *Macaca mulatta*: Kapsalis & Berman, 1996; Japanese macaques, *Macaca fuscata*: Ventura, Majolo, Koyama, Hardie, & Schino, 2006; Barbary macaques, *Macaca sylvanus*: Carne, Wiper, & Semple, 2011; tufted capuchin monkeys, *Sapajus apella*: Tiddi, Aureli, di Sorrentino, Janson, & Schino, 2011). Although GG-rubbing in female bonobos is multifunctional (Hohmann & Fruth, 2000), it occurs most often during feeding and may reduce tension and enable females to feed together (Fruth & Hohmann, 2006; Furuichi, 1989; Hohmann & Fruth, 2000; Kuroda, 1980; Paoli et al., 2007; Parish, 1994; Ryu, Hill, & Furuichi, 2015). These affiliative interactions might enable females to tolerate one another and to be in the same party, thereby indirectly contributing to the formation of female coalitions.

Reciprocal agonistic support is observed in several animal species (e.g. bonnet macaques, *Macaca radiata*: Silk, 1992; chimpanzees: Watts, 2002; Mitani, 2006; coatis, *Nasua nasua*: Romero & Aureli, 2008; ravens, *Corvus corax*: Fraser & Bugnyar, 2012). The agonistic support of bonobos in five captive groups was highly reciprocal at the group level, but the result was mostly a side-effect of strong correlations between support and dominance (Stevens, Vervaecke, de Vries, & van Elsacker, 2005; Vervaecke, de Vries, & van Elsacker, 2000a). Reciprocal exchange of support was found only in one group after controlling for rank effect (Stevens et al., 2005; Vervaecke et al., 2000a). In our study, wild female bonobos did not support each other reciprocally. These tendencies might indicate that reciprocal altruism had little effect on the evolution of female coalition in bonobos. Nonreciprocal support may be due to unidirectional relationships within a dyad in which older females support younger ones.

In this study, all observed female coalitions resulted in the target male displaying submissive behaviours. Females of all age categories could win against males more easily when they formed coalitions than when they confronted males alone. This benefit of forming coalitions might be greater for young females than for old females since young females were less likely to win against males in dyadic aggression than were old females. Furthermore, female coalitions may benefit all females by making males refrain from attacking females because of the risk of counteraggression (Smuts & Smuts, 1993). Participating in female coalitions might be a low-risk behaviour because males never opposed female coalitions. Since all females in the coalition gained benefits from forming coalitions, female coalitions might be formed for mutual individual benefits (or mutualism: Clutton-Brock, 2009).

Unidirectional agonistic support from older to younger females might be explained by benefits to both females. For younger females, who might find it difficult to dominate males if they confront males by themselves, agonistic support from older females might enable them to stay central to the party without suffering male harassment. Since older females tend to be dominant and stay in the best feeding positions (Furuichi, 1989, 2011; Parish, 1994), young females may experience feeding disadvantage to some extent. However, the benefit of receiving agonistic support might enhance the advantage of associating with older females, including feeding priority over males (Furuichi, 1997; Parish, 1994; White & Wood, 2007), thereby compensating for the feeding disadvantage among females. Some behaviours of young females indicate that they are attracted to older females; young females actively associate with and follow older females (Idani 1991; Sakamaki et al., 2015) and beg for abundant fruit from them to confirm their tolerance (Goldstone, Sommer, Nurmi, Stephens, & Fruth, 2016; Yamamoto, 2015).

On the other hand, for older females, attracting younger females around them might be beneficial in increasing the mating success of their sons, since a male's mating success is higher when his mother is in the same party (Surbeck, Mundry, & Hohmann, 2011). It might also be the reason why old females stay in the central part of the party (Furuichi, 1989, 2011; Parish, 1996; Parish & de Waal, 2000) and control party movement (Furuichi, 2009, 2011). Old females might actively support younger females not only because they gain the direct benefit of winning against males but also because they are able to enhance the benefit of group living by attracting other females around them.

Our results suggest that female coalitions in bonobos might have evolved as a counterstrategy against male harassment. Females might choose their coalition partners based not on affiliative relationship or reciprocity but, rather, on mutualism. The importance of coalition partners largely affects the shape of female social relationships in nonhuman primates (van Hooff & van Schaik, 1992; van Schaik, 1989; Sterck et al., 1997; Wrangham, 1980). Additionally, in bonobos, female coalitions might lead to the development of affiliative behaviours and high tolerance among females. There may be positive feedback between female coalition formation and female gregariousness, wherein the benefits of forming coalitions may increase gregariousness, and gregariousness promotes the formation of female coalitions. There may be additional positive feedback between female gregariousness and female affiliative interactions for tolerance, where the importance of being gregarious might lead females to develop tolerant behaviours (i.e. GG-rubbing and frequent grooming among females). Although there was no direct connection between affiliative behaviours and coalition formation, the strong female social bonds in female dispersal societies might have been established and reinforced by these positive feedbacks. When male efforts to dominate or coerce females were no longer useful due to female resistance, males might have had to

develop good relationships with their mothers and other females to attain mating success rather than behaving aggressively towards females (Furuichi, 1989; Hare, Wobber, & Wrangham, 2012; Kano, 1992, 1996; Surbeck et al., 2011).

Although wild female chimpanzees rarely form coalitions, female coalitions are observed relatively often at some sites where females are more gregarious (e.g. Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2006). The pattern of female coalitions observed in Budongo forest chimpanzees is very similar to our results. Newton-Fisher (2006) observed nine female coalitions retaliating against male harassment. Most agonistic support was directed from dominant females towards subordinate females, suggesting that there might not be a reciprocal relationship. These similarities suggest that patterns of female coalitions might not have evolved specifically in bonobos but, rather, are common among *Pan* species.

Variation in female gregariousness, which may be caused by differences in food abundance, could be pivotal to promoting or constraining female coalitions (Parish, 1996). Considerable behavioural diversity is reported within the genus *Pan* (Boesch, Hohmann, & Marchant, 2002; Whiten et al., 1999). Most studies of wild bonobos, including ours, have been conducted in dense forest habitats where food availability is relatively high and stable (White, 1998; White & Wrangham, 1988). However, bonobos live in diverse environments, including mosaic forests where conservation, habituation and research activities have recently begun (Inogwabini, Bewa, Longwango, Abokome, & Vuvu, 2008; Narat, Pennec, Simmen, Ngawolo, & Krief, 2015; Serckx et al., 2014). Comparison of female behaviours across various differing environments will be important for revealing the evolution of female social relationships and coalitions in bonobos.

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