Animal Behaviour 119 (2016) 27–35

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Nahoko Tokuyama*, Takeshi Furuichi

Primate Research Institute, Kyoto University, Kyoto, Japan

ARTICLE INFO

Article history:
Received 28 February 2016
Initial acceptance 30 March 2016
Final acceptance 2 June 2016
Available online 19 July 2016
MS. number: 16-00167R

Keywords:
agonistic interaction
bonobo
cooperative behaviour
female coalition
mutualism
Pan paniscus
social bond

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.

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

* Correspondence: N. Tokuyama, Primate Research Institute, Kyoto University, 41-2 Kanrin, Inuyama, Aichi, 484-8506, Japan.
E-mail address: tokuyama.nahoko.47x@kyoto-u.jp (N. Tokuyama).

http://dx.doi.org/10.1016/j.anbehav.2016.06.021
0003-3472/

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 Taï 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 (Taï 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