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A Case Study of Conflict Management in Bonobos: How Does a Bonobo (*Pan paniscus*) Mother Manage Conflicts between Her Sons and Her Female Coalition Partner?

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Key Words

Bonobo · *Pan paniscus* · Mother-son relationship · Female coalition · Maternal support · Conflict management · Dilemma

Abstract

Female coalitions are an important part of the social organization of bonobos. The strength of the mother-son relationship is another essential part of this social structure. A bonobo mother is therefore facing a dilemma when a conflict arises between her sons and her female coalition partners. Will she take her coalition partner's side and favour the social organization of the group or support her son in order to defend her offspring? In order to address this issue, we performed an observational study of the captive group at Planckendael (Belgium) and used social grooming and proximity to assess the relationship between individuals. As a case study, we focused on the relationships between Hortense, one of the group's mothers, her 3 sons Redi, Vifijo and Zamba, and her coalition partner Hermien. Surprisingly, we observed that Hortense preferentially supported her female coalition partner. For Hortense's social status in the group, it may be more important to maintain the strong relationship with her higher-ranking female coalition partner than to support her sons.

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Introduction

The relationships between female bonobos are central in their social organization [Kuroda, 1980; Furuichi, 1987, 1989; White, 1988; Idani, 1991; Kano, 1992; Parish, 1994, 1996; Parish and de Waal, 2000]. Coalitions between female relatives are

often impossible due to female transfers [Kano, 1987; Furuichi, 1989] between groups but, in spite of this limitation, groups are structured around supportive relationships between unrelated adult females [Badrian and Badrian, 1984; White, 1988; Kano, 1992; Furuichi and Ihobe, 1994; Parish, 1994, 1996; de Waal, 1995; Furuichi, 1997; Parish and de Waal, 2000; Vervaecke et al., 2000b, c; Stevens et al., 2006]. These coalitions provide their members with a series of advantages, such as a preferential access to food resources and the possibility for females to give birth at younger ages, which result in increased reproductive success [Parish, 1996; Hohmann et al., 1999]. Moreover, the frequency of supportive behaviours between females may also contribute to increasing their hierarchical status [Parish, 1994, 1996; Vervaecke et al., 1999, 2000b, c; Stevens et al., 2001, 2007]. The social organization of bonobos is therefore generally described as egalitarian and based on female dominance [Kuroda, 1980; Kano, 1996; Parish, 1996; Furuichi, 1997; Fruth et al., 1999; Parish and de Waal, 2000; Vervaecke et al., 2000a; Stevens et al., 2007]. Female dominance is not systematic, however [Vervaecke et al., 1999, 2000a; Stevens et al., 2007], and older females tend to dominate the younger ones [Furuichi, 1997].

The social organization in bonobos is also centred on the relationships between mother and sons [Kuroda, 1989; Ihobe, 1992; Kano, 1992, 1996; Furuichi and Ihobe, 1994; Furuichi, 1997]. Even though proximity between mother and sons tends to decline with age, adolescent and adult males maintain close and strong grooming relationships with their mother [Kano, 1982, 1992, 1996; Furuichi, 1989, 1997; Kuroda, 1989; Ihobe, 1992; Furuichi and Ihobe, 1994].

Bonobo mothers also seem to play an essential role in the hierarchical status of their sons. Indeed, Furuichi [1997] reported that changes in dominance between high-ranking males are often preceded by a corresponding change in the status of their mothers. When a male achieves higher hierarchical status, he remains in the spatial centre of the group, which may provide him with better access to receptive females and increase his reproductive success.

Given the strong affiliative bonds that exist between mothers and their sons and within female coalitions, a conflict between one of her sons and one of her female partners would put a bonobo mother in a difficult situation. Indeed, either she supports her partner, and then acts against her own son's interests, or she supports her son and jeopardizes the coalition that provides her with a high hierarchical status. Of course, one obvious solution would consist of simply not intervening. Another possibility would be to try to stop the conflict before anyone is injured and without directly supporting any of the opponents. The bonobo mother would then preserve her female coalition without acting against her son.

In this paper, we had the unique opportunity to study a group comprising a mother of 3 sons, Hortense, who was having a long-term supportive relationship with another female in the group.

In this case study, we were interested in the way Hortense would manage a conflict between one of her sons and her female coalition partner. Female coalitions, on the one hand, and the strong relationships between mothers and sons, on the other, are two of the most fundamental structures of bonobo social organization. We therefore asked whether a mother would choose to assist her female coalition partner or rather support her sons in order to defend her offspring.

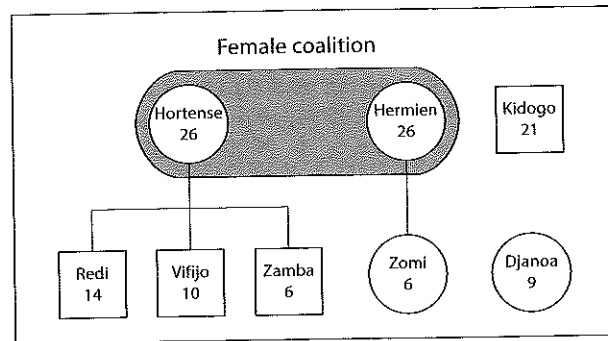


Fig. 1. Composition of Planckendael's bonobo group. The lines represent kinship.

Method

Study Group

At the time of study, the Planckendael group consisted of 8 members, including 3 females, 3 males and 2 juveniles.

Figure 1 shows the group and kinship relationships between individuals. Hermien and Hortense formed a female coalition and were at the top of the hierarchy [De Lathouwers, pers. commun., February 2004]. Hortense had 3 sons: Redi (14 years old), Vifijo (10 years old) and Zamba (6 years old). Hermien had 1 daughter: Zomi (6 years old). Kidogo, a 21-year-old male, and Djanoo, a 9-year-old female, were not related to Hermien or Hortense.

Data Collection

Quantitative analyses in this study are based on observations conducted in the indoor enclosure between mid-January and the end of March 2004. During the summer, the group has access to an outdoor enclosure. Observations started at approximately 9 a.m. when the bonobos got their breakfast, and finished around 5 p.m. after the evening meal, when the bonobos started to make their nests. Observations therefore covered most of the grooming behaviour and supportive activities performed during the daytime. The total observation time amounts to approximately 400 h.

Support and Intervention

All occurrences of agonistic, supportive and affiliative behaviours were recorded by means of the 'all occurrences sampling' method [Altmann, 1974]. A 'support' was recorded if any individual intervened, using an agonistic behaviour (excluding pestering), at most 30 s after an agonistic interaction (including pestering) between at least 2 other individuals, in order to provide assistance either in attack or in defence [de Waal and Luttrell, 1986].

Importantly, 'supports' constitute a subcategory of 'interventions'. Indeed, an individual could merely intervene during a conflict between two other individuals without showing any agonistic behaviour directed towards one of the opponents, as an undirected display for instance. We referred to a support only when an agonistic behavior was directed towards one of the opponents.

Grooming

In order to assess the quality of the relationships between individuals, we recorded the duration of each grooming sequence as well as the proximity between any two individuals. A grooming sequence was defined as a continuous period of social grooming between any two individuals, which was neither interrupted by a pause of more than 30 s nor by any other groom-

Table 1. Hortense's interventions and supports (% , numbers in parentheses) depending on the opponents

	Redi (son No. 1)	Vifijo (son No. 2)	Zamba (son No. 3)	Total
Hermien				
Interventions	56 (31/55)	8 (2/26)	50 (1/2)	41 (34/83)
Supports	49 (27/55) 27 for Hermien 0 for Redy	0 (0/26)	0 (0/2)	33 (27/83)
Kidogo				
Interventions	17 (1/6)	0 (0/1)	0 (0/1)	12 (1/8)
Supports	0 (0/6)	0 (0/1)	0 (0/1)	0 (0/8)
Djanoo				
Interventions	6 (6/102)	0 (0/5)	100 (1/1)	6 (7/108)
Supports	4 (4/102) 2 for Djanoo 2 for Redy	0 (0/5)	100 (1/1) 0 for Djanoo 1 for Zamba	5 (5/108)
Total				
Interventions	23 (38/163)	6 (2/32)	50 (2/4)	21 (42/199)
Supports	19 (31/163)	0 (0/32)	25 (1/4)	16 (32/199)

The percentages have been calculated based on the total number of each kind of conflicts. For instance, Hortense intervened in 31 out of 55 conflicts between Hermien and Redi (i.e. 56%). As can be read in the last column, she intervened in 41% of the 83 conflicts involving Hermien.

ing or any other activity. Grooming was recorded by means of the 'all occurrences sampling' method [Altmann, 1974].

Spatial Proximity

The assessment of spatial proximity between Hortense and each of her sons was based on the scan sampling method [Altmann, 1974], representing the time spent by Hortense with each of the other group members. Every 15 min, we recorded the identity of any two individuals which were less than 1 m from each other.

Statistical Analyses

We did not apply statistical analyses to grooming and proximity data as they did not constitute the main focus of our study. Concerning the frequencies of Hortense's interventions and supportive behaviours towards the different opponents, we used Pearson's χ^2 tests to assess statistical significance.

Results

Hortense's Interventions and Supportive Behaviours during Conflicts

Recall first that supports are a subcategory of interventions. The number of supports is therefore necessarily inferior to or equals the number of interventions. Table 1 suggests that Hortense did not intervene often in conflicts, except when Hermien was involved. When she did intervene, however, it was mostly to support one of the opponents. She seldom intervened without supporting one of the opponents.

Table 2. Frequencies of Hortense's supports in favour of the individual in the column head

Hermien (female)	Kidogo (male)	Djanao (female)	Redi (son No. 1)	Vifijo (son No. 2)	Zamba (son No. 3)
33% (27/83)	0% (0/8)	2% (2/108)	1% (2/181)	0% (0/49)	11% (1/9)

The percentages have been computed based on the total number of conflicts in which the individual mentioned in the column head was involved. For instance, Hortense supported Hermien in 27 out of 83 conflicts, i.e. in 33% of the cases.

Table 3. Distribution of grooming and proximity between Hortense and each of the other group members

	Hermien (female)	Djanao (female)	Kidogo (male)	Redi (son No. 1)	Vifijo (son No. 2)	Zamba (son No. 3)
Grooming	26% (182)	4% (25)	3% (21)	16% (115)	38% (272)	13% (93)
Proximity	8% (22)	6% (16)	5% (13)	5% (13)	14% (37)	52% (135)

Active grooming from Hortense is shown in the first row; numbers in parentheses refer to the number of minutes spent with each individual. The second row indicates the percentages of scans in which Hortense was close to each group member (scans in which she was alone are not taken into account); numbers in parentheses refer to frequencies.

More specifically, a Pearson χ^2 test performed on the frequencies of supports from Hortense (table 2) indicated that Hermien received more support from her than any other member of the group ($\chi^2 = 65.11$, d.f. = 4, $p < 0.001$).

Another Pearson χ^2 test confirmed that Hortense intervened significantly more often in the case of a conflict opposing one of her sons with Hermien (41% of the conflicts, $\chi^2 = 3.31$, d.f. = 1, $p < 0.0001$) than with Djanao, a young female who had recently arrived in the group (6% of conflicts). The conflicts involving Hermien were also the most likely to elicit Hortense's supportive behaviour, even though these conflicts were less frequent than those in which Djanao was involved. Djanao was nevertheless the only individual against whom Hortense supported her sons. Indeed, Hortense supported Redi twice and Zamba once against Djanao. There were only a few conflicts involving Kidogo, an unrelated adult male, and Hortense never supported one of the opponents.

Grooming and Spatial Proximity

As can be seen in table 3, Hortense's son Vifijo received most of her grooming (38%), and Hermien, her coalition partner, comes second with 26% of Hortense's grooming. Concerning spatial proximity, Zamba, Hortense's youngest son, is the one who spent most time (52% of scans) within a distance of less than 1 m from his mother. By contrast, Hortense and Hermien were in close proximity in only 8% of scans.

Discussion

Our goal was to study how, in the specific social group that we observed, a bonobo mother deals with a conflict between one of her sons and her female coalition partner. To address this issue, we observed affiliative and supportive behaviours between a bonobo mother and the other related and unrelated group members. We will first discuss our observations concerning grooming, proximity and Hortense's behaviour in case of a conflict. Then, we propose three possible interpretations of the fact that her female coalition partner, Hermien, happens to be the main recipient of her supportive behaviour.

Grooming and Social Proximity

By and large, grooming generates bonds that constitute the basis upon which coalitions and supportive behaviours can grow. Indeed, we observed a considerable amount of grooming between Hortense and Hermien. Concerning spatial proximity, unlike the observations of Furuichi and Ihobe [1994] on the close female bonds in the wild, we observed that Hortense did not spend most of her time with Hermien. Together, these observations suggest that Hortense and Hermien did not stay close to each other without engaging in social behaviour.

Dilemma at the Time of Conflicts?

The particular relationship between mother and sons and the role of female coalitions in bonobo social organization raises the following question: how would Hortense react in the event of a conflict between Hermien and one of her sons? An obvious possibility would be that Hortense would limit her intervention in an attempt to stop the conflict so that nobody gets injured but without overtly taking side. This way, she should not have to act against her son's interests or to jeopardize the female coalition.

Surprisingly, we observed that, while Hortense did not often intervene during conflicts (42 times in 199 conflicts), when she did, it was mostly to support one of the opponents (32 supports in 42 interventions). Most of the time, she directly supported Hermien and therefore took side against her own son. Three potential explanations can be proposed in order to account for this surprising result.

First, it is important to look at the reasons for the frequent occurrence of conflicts between Redi and Hermien. They did not originate in a competition for resources, but rather in Redi's pestering. Interestingly, when Hermien was the subject of this pestering, she, several times, made her way towards Hortense and embraced her. This behaviour strongly reminds one of the stretching-out behaviour observed by de Waal and van Hooff [1981] in chimpanzees. Redi never behaved that way. Hortense's supports to Hermien might then also be explained by Hermien's embracing behaviour.

Second, the relationship between Hortense and her sons' opponent appears to be a major determinant of her behaviour. Indeed, even though the conflicts between Redi and Djanao (most often due to Redi's pestering) were twice as frequent as the conflicts between Hermien and Redi, Hortense almost never intervened in the former cases. This difference could be explained by the weakness of the bond between Djanao and Hortense. This weakness is also reflected in the amount of grooming: Hortense provided a lot more grooming to Hermien (26% of all her grooming) than to Djanao (4% of all her grooming). While Hermien and Hortense have lived in the same group for several years, Djanao is a newcomer. She did not have the opportu-

nity to build strong affiliative bonds with Hortense and Hermien, like female bonobos usually do [Idani, 1991; Kano, 1992; Parish, 1996; Furuichi, 1997; Vervaecke et al., 2000b, c; Hohmann and Fruth, 2002].

This observation confirms the usual association between the frequency of grooming and the propensity to support [Seyfarth, 1977; Vervaecke et al., 2000b]. The more grooming is observed between two individuals, the greater the propensity to support each other will be. We indeed observed that Hortense tended to support Hermien with whom she exchanged a large amount of grooming, while she did not support Djanoa with whom she did not exchange much grooming.

Therefore, the origin of the conflicts (pestering) may not be the only reason for Hortense's support. The nature and the quality of the relationship between Hortense and the other female may also have been a determinant in Hortense's reaction.

Finally, we would like to propose a third, more cognitive, potential explanation for Hortense's behaviour, with the caveat that this interpretation probably makes sense in this specific social group only, given the individual characteristics of its members. As this interpretation is not directly based on observational data, it must thus be considered with caution. We observed that Hortense never injured her son when supporting Hermien. Although Hortense's reaction was more impressive and violent than Hermien's reaction, she always stopped before actually hurting her son. One may therefore consider that, in acting this way, Hortense exerted some control over the attacks against her son and prevented Hermien injuring Redi in a fit of rage. Indeed, if Hortense simply refrained from intervening, Hermien may have continued the conflict and become a real danger to Redi as she could injure him. As a consequence, by supporting Hermien, Hortense may limit her agonistic behaviours towards Redi and, paradoxically, so protect her son. This assumption does not necessarily imply that Hortense has a 'machievellian mind'; she could have merely observed that her support towards Hermien tended to protect her sons from potential injuries and learned to behave accordingly.

To sum up, our study emphasizes the need for female bonobos to balance their support between their sons and their female coalition partners. Further studies are needed in order to see in which way such behaviour may be influenced by the social status of the individuals involved in conflicts.

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