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Mother-Offspring Spatial Relationships in Wild Eastern Chimpanzees (*Pan troglodytes schweinfurthii*)

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Abstract

Young chimpanzees (*Pan troglodytes schweinfurthii*), need to learn social behaviors in order to successfully establish stable social interactions. It is accepted that genetics, social environment and maternal conduct determine the social ontogeny and future social success of younglings. Mothers with dependent offspring are less gregarious than females and males. According to the "infant safety" hypothesis, mothers are less gregarious in order to minimize the dangers surrounding the offspring, such as the threat that males pose to infants. Studying mother-offspring spatial relationships can give good indications of maternal care and vigilance. In this study, we investigated how maternal association patterns (either loner or in mixed or female-only parties), and other maternal characteristics, such as rank and age/experience, correlate with mother-offspring spatial relationships. We observed 10 wild mother-infant dyads in the Budongo Forest, Uganda, during 6 months. We measured maternal association patterns, mother-to-offspring distance and proximity maintenance towards the infants. Our results suggested that mothers spend more time in female parties and mixed parties than alone. This observation could indicate the need to socialize the infant. The spatial relationship was influenced by maternal association patterns. The presence of males reduced the mother-to-offspring distance and the presence of females increased it. Also, more experienced mothers maintained higher proximity with their infant than less experienced mothers. This study reveals that there is a relation between maternal characteristics and the social environment surrounding mothers and offspring. Further investigation should extend the area of research to other communities, since it has been shown that ecological and demographic factors influence party sizes, which in turn seem to affect maternal behaviors. A better understanding of how mother-to-offspring behavior is determined by social situations and maternal experience and social status is necessary in primate research.

INTRODUCTION

In long-lived social mammals like primates, social behavior is dictated by innate and acquired behavioral patterns. Individuals living in organized societies need to deal more specifically with the development of social behaviors and cognitive abilities (Deputte, 2000). It is accepted that maternal behavior, genetics and social environment all contribute in influencing this development (De Lathouwers, 2003; De Lathouwers and Van Elsacker, 2004; Deputte, 2000).

Partly, social ontogeny is influenced by the social environment, which is determined by social partners. For example, immature rhesus monkeys need to interact with other group members to develop proficient social behaviors (Harry F. and Harlow, 1962; Hemelrijk and Kogel, 1989). On the other hand living in a complex social group poses serious threats on the offspring's safety, mainly by aggressions from male conspecifics (e.g. infanticide). Moreover, fission-fusion societies of chimpanzee communities may have an impact on the mother-infant relationships and on the ontogeny of sociability (Hemelrijk and Kogel, 1989). These organized social environments require from individuals to develop good social behavioral repertoire and a network of social relationships (Deputte, 2000).

However, studies demonstrate that infant social opportunities and safety depend on the personal characteristics of the mother (*i.e.* her "maternal styles" Altmann, 1980) and her social position in the group (Hemelrijk and Kogel, 1989). Mothers provide the infants with all their needs: thermoregulatory assistance, ectoparasite removal and protection against potential predators and dangerous conspecifics. These tasks are risky and demand a dedication of time and energy while maintaining the everyday life activities, like foraging (Lancaster et al., 2010).

Mothers are key in the early socialization of their offspring (Bardi and Huffman, 2002, 2006; De Lathouwers and Van Elsacker, 2004; Fairbanks and McGuire, 1988), and thus influence their future reproductive success (Clutton-Brock, 1991; Otali and Gilchrist, 2006) (the infant integration hypothesis). In primates, maternal behaviors directly influence the younglings' curiosity, namely their interest to initiate contacts with other group members or to explore the environment (Bardi and Huffman, 2002). Maternal subgrouping patterns may facilitate the social interactions of infants (Murray et al., 2014). Female chimpanzees are less gregarious than males, and that within females, the least gregarious are those with dependent offspring (Wrangham, 2000; Otali and Gilchrist, 2006; Goodall, 1986). This is explained by the infant safety hypothesis:

because of the vulnerability of infants and the threat that aggressive males pose (Otali and Gilchrist, 2006).

During the first six months of life, the mothers with daughters are less gregarious than the ones with sons (Murray et al., 2014). This announces the sex differences in adult social behaviors. Adult male chimpanzees get more involved in the "politics" and are more integrated into the community, whereas many females may emigrate at adolescence (Murray et al., 2014). Interestingly, maternal association patterns vary as the youngster ages. In semi-captive chimpanzees, the mother associates more with females than with males when babies are less than two-year-old. But as the infant grows older, the association with males increases. Interestingly, this shift occurs a year or so before the mother resumes the sexual cycling (Horvat and Kraemer, 1981). This maternal strategy seems to be crucial to maximize the survival and future reproductive success of the offspring, by familiarizing it to members of the community and as a preparation to a mother's intense social relationship with males (Horvat and Kraemer, 1981; Kummer, 1989; Otali and Gilchrist, 2006).

Studying the effect of other group members on mother-infant spatial relationships may give clues on how a mother adjusts her behavior towards the safety or the integration of her infant. How do mothers deal with this dilemma between infant security and providing social opportunities, especially in chimpanzees, where conspecific aggressions by males are frequent (Trevathan, 1987; Wrangham and Peterson, 1996)? Different factors seem to be involved in shaping maternal choices in association patterns and maternal care, shown for example by controlling the distance between herself and her offspring.

The spatial relationship between mothers and their offspring, which is particularly sensitive to proximal threats (i.e. predators, other group members), represents a good indicator of maternal care and maternal vigilance (Fairbanks, 1996). In general, maternal vigilance is described as the simple movement of the head or scanning the surroundings (Kutsukake, 2006). Studies on vigilance behaviors mostly observe threats like predation. Intriguingly, within-group threats like conspecific aggressions are relatively ignored (Kutsukake, 2006). It is interesting to know how much the mother keeps an eye out for threats but also how she keeps ready to protect the infant. To observe that, it is necessary to consider vigilance of mothers as a physical and dynamic factor. Indeed, mothers may adjust their behavior – and thus the proximity – with their offspring depending on the context. The distance between a mother and her offspring can be used as an index of attention or protection given by a mother to her infant (Cameron et al., 2003; Otali and

Gilchrist, 2006). Not only the distance itself might be important, but also if the mother of the infant is actively reducing this distance, then it is about proximity maintenance.

Differences within mothers include day-to-day variations, like maternal association patterns, described by the party composition at a particular time – absence or presence of sub-adult and adult males and females. It is widely accepted that males are more aggressive than females, and often aggress females (Wrangham and Peterson, 1996). In general, mothers associate less with males than with females (Kappeler, 2000; Otali and Gilchrist, 2006).

The spatial relation to the infant might also vary depending on the rank and age of the mother. Dominance hierarchies among female chimpanzees were not given any importance until it was suggested that high-ranking females have significantly higher infant survival (Pusey et al., 1997). Studies on rhesus monkeys and chimpanzees demonstrate that mothers who receive more aggressions by conspecifics tend to keep their infant closer, leading to a reduction of the infant's social interactions with peers (Hemelrijk and Kogel, 1989; Simpson and Howe, 1986). Also, in olive baboons (*Papio anubis*), low-ranking females are subject to frequent aggressions from other females (Smuts and Nicolson, 1989), observations that are attributed to chronic stress and low reproductive success.

The age of the mother reflect maternal experience (De Lathouwers, 2003). Some suggest that older mothers are more protective and tend to promote distance less than young mothers (De Lathouwers, 2003), while others claim that mothers that reared a larger number of offspring are more rejecting (Hemelrijk and Kogel, 1989). This same study observed that infants of those mothers were less involved in social play, probably because of the presence of siblings to play with (Hemelrijk and Kogel, 1989). Understanding how maternal characteristics such as age and rank, affect mother-infant interactions should give insights on the role of the mother to foster the sociability of young chimpanzees.

In summary, the social integration of infants is important for the development of their social skills (infant integration hypothesis) yet avoiding aggressions from other group members, especially males and higher-ranking females (infant safety hypothesis). By controlling the distance to their infant (spatial relationship), mothers can vary the degree of infant safety and provide opportunity for social interactions. Mother-infant spatial relationships might vary depending on the mother's association patterns, age and dominance rank.

Mothers are less gregarious than other females and males, thus we firstly hypothesized that maternal association patterns are dictated by the infant safety and social integrability. Thus, we predict that (a) mothers will associate more often with only females (infant integration) or prefer staying alone than with parties where males are present (infant safety).

Secondly, we propose that mothers adjust the spatial relationship to their offspring depending on the party composition. We predict that mothers (b) keep a shorter distance to their infant if the number of males in the party increases (infant safety) than in the presence of only females (infant integration). Additionally, we predict that (c) in the presence of males the mother actively decreases the distance to the infant (infant safety). Overall we expect (d) that more experienced mothers keep a shorter distance to their infants than less experience mothers, and (e) that higher-ranked mothers keep a bigger distance to the infant than lower ranked ones.

MATERIALS AND METHODS

Field site and study subjects

We observed chimpanzee mother-infant dyads from the Sonso community of the Budongo Forest, Uganda, between July 2016 and December 2016. As of 2016, the group size of the Sonso community was 71 individuals, with 25 adult females and 10 adult males. The Budongo Forest Reserve is situated between 1°37N – 2°03N and 31°22 – 31°46E and comprises 435 km^2 of moist, semi-deciduous tropical rain forest. Habituation to human presence started in 1992 (Reynolds, 2005). The subjects are 10 mother-infant pairs of wild eastern chimpanzees (*Pan troglodytes* schweinfurthii) of the Sonso community. The sample included 8 male and 2 female infants. At the beginning of the study, estimated maternal age ranged from 19 to 41 years and infant age ranged from 8 to 76 months (see Table 1). All infants were still not weaned during the data collection.

Table 1 Characteristics and observation time of each mother focal (alphabetical order)

Mother	Average mother age (y)	Average infant age (y)	Infant sex[a]	Mother rank[b]	Location of range in community[c]	Number of follows	Observation time (h)
GL	40.3	3.38	M	7	Peripheral	9	17.1
HT	38.2	2.91	F	1	Peripheral	10	26.5
KL	37.2	1.98	M	5	Central	10	24.5
KU	37.2	2.51	M	4	Central	11	26.8
KW	35.3	3.27	M	3	Central	10	23.7
KY	33.2	1.82	M	2	Peripheral	9	21.8
ML	41.4	1.07	M	6	Peripheral	5	11.2
OK	20.2	1.97	M	10	Central	11	28.9
RS	19.2	2.93	M	9	Central	9	25.4
TJ	32.2	6.49	F	8	Peripheral	5	10.3

[a] Was not used for the analysis because of too many male infants

[b] Determined after asking each field assistant to rank the mother between each other. No research on Sonso females gives a detailed review of female-female hierarchy

[c] Based on the unpublished data of Christof Neumann, who calculated centrality indexes for every female with BCFS' long-term data

Data collection

We did all day follows on the mother-offspring pair noting down general behaviours like resting, foraging, grooming in a one-zero method (Altmann, 1974), with a time interval of 5 minutes. Data when the mother was travelling was excluded because of the difficulty of observation. We took party composition (PC) in 5 minutes scans including all adult and sub-adult males and females present within 30 meters of the focal to observe for potential effects of the PC on mother-infant spatial relationships. Juveniles were not included in party composition data because another study showed they did not affect the mother-to-offspring distance (Otali and Gilchrist, 2006). This allowed us to calculate the frequency of time a mother spent in different parties (alone, with females only, with males only, mixed group). We used mother-to-offspring distance and proximity maintenance to define the mother-infant spatial relationship. The estimated mother-infant distance (meters) was noted every 5 minutes. As we were interested in how the mother controls the spatial relationship, we defined the proximity maintenance as the number of approaches made by the mother only. Every time the mother-infant distance was reduced or increased – by movements of the mother or the infant –, we noted down "approaching" or "leaving", with the identity (mother/infant).

Statistical analysis

To test the influence of focal characteristics and party composition on mother-offspring spatial relationships, we used generalized linear mixed models (GLMM) with binomial error distribution to enable the appropriate use of random terms. Our response variables were proximity maintenance, defined as the probability of mothers approaching their infant in a binary way (0: infant approaching, 1: mother approaching), and within dyad distance, in meters. We fitted mother identity (n=10) and date (n=76) as random intercept terms to all our models. In both models, we tested the interaction of adult males and adult females present in the party composition. Predictor variables as well as factors accounted as fixed effects in the statistic models are shown in Table 2 below. Field assistants and researchers, who worked at the station for several years, estimated the maternal rank. Maternal social experience refers to the years since a field assistant first saw the mother in the community. The more years, the more social experience a mother has. Maternal experience, which increases with mother age (De Lathouwers, 2003), is defined as the number of offspring who reached 5 years old for each individual mother. Infant age is used as a control predictor since it has an effect on the spatial

relationship (Altmann, 1980; Maestripieri et al., 2002; Napier and Napier, 1994; Plooij, 1984). Therefore it is important to have it in the model because we can expect an effect. All test were two-tailed with significance level $P<0.05$. Data were analyzed using the package lme4 in R 3.3.2 with RStudio 1.0.136.

Table 2 Variables used as fixed effects

Variable	Range
Maternal age	19 – 41 years
Infant age	8 – 76 months
Maternal dominance rank	1 – 10 (high – low ranked)
Maternal social experience[A]	6 – 24 years
Maternal experience[B]	0 – 4
Presence or absence of males (binary)	Absent/present
Number of males (quantitative)	0 – 9
Number of females	0 – 13

[A] Years since an individual was first observed by researchers or field assistants

[B] Defined as the number of infants reaching 5 years of age for each individual mother (*De Lathouwers and Van Elsacker, 2004*)

As the focal mothers were more than half of the time in parties without any males (57%) – from 1 to 9 males, the number of observations stays very low (n=15–132) –, we decided to run two separate statistic tests for each response variable taking the number of males as quantitative data (from 0 to 9) for one and as binary data (0, no male present; 1, one or more males present) for the other, to check for consistency. Another study with wild chimpanzees showed that mother-to-infant distance is lower in the presence of males (as binary) and that this distance decreases as the number of males increases (as quantitative, Otali and Gilchrist, 2006). Furthermore, by doing so, we are able to see the importance of the number of females in the party composition.

To assess the stability of our models, we tested for potential influential cases that might alter the conclusions of the analysis. To do so we created 10 datasets in which each mother/infant dyad was excluded in turn. We fitted full and null models on these 10 datasets. We compared the parameter estimates of these models and the likelihood ratio test with the result of the full

model and found that excluding any individual did not affect the conclusions with regards to the mother approaches and the mother to infant distance.

RESULTS

Maternal association patterns

By combining the infant safety and the infant integration hypothesis, we predicted that mothers would spend more time in female-only parties or alone than in mixed or male-only parties. This prediction is not verified. Fig. 1 shows the time spent in each subgroup composition. Mothers associated more often with females than with males (*T-test*, P=0, n=2000 scans, Table 3) or alone (*T-test*, P<0.01, n=2000 scans, Table 3). They also spent significantly more time in mixed parties than with only males or alone (*T-test*, P=0, n=2000 scans, Table 3). Additionally, 53% of the females associated with other mothers with dependent offspring (*T-test*, *P*<0.0001, n=2000 scans).

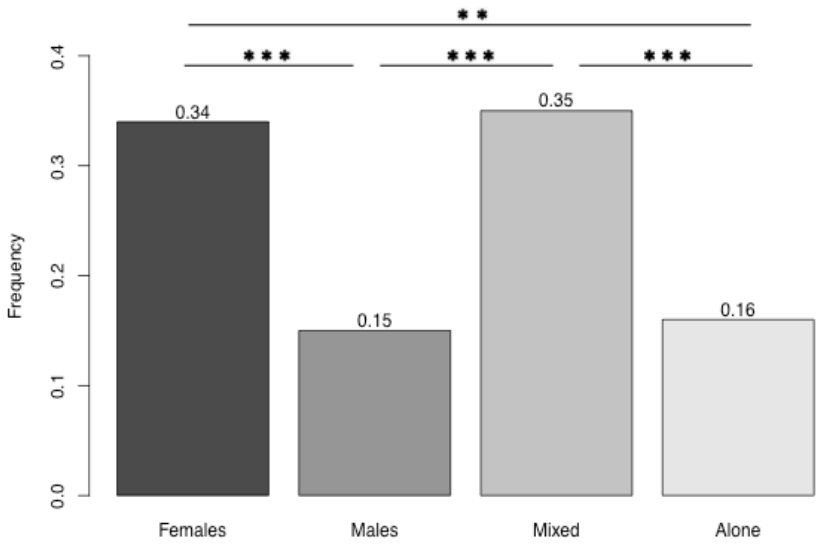

Figure 1 Frequency of time spent in each subgroup composition by the focal mothers – black: only with females, dark grey: only with males, light grey: both females and males, white: alone. Two thirds of their time was significantly spent with female parties or mixed parties (*** p = 0, ** p = 0.008).

Table 3 *T-tests* showing differences in party composition. Significant results are in bold.

var1	var2	t.value	df	p.value
Females	**Males**	**5.128**	**14.46919**	**0*** **
Females	Both	-1.758	17.85803	0.096
Females	**Alone**	**3.023**	**17.40737**	**0.008** **
Males	**Both**	**-7.671**	**15.26287**	**0*** **
Males	Alone	-1.979	16.1298	0.065
Both	**Alone**	**5.11**	**17.8324**	**0*** **

Number of adult males and females vs mother-to-offspring distance

The analysis of the data supports our prediction that the distance separating mothers and infants is lower when the number of males increases – thus, in the presence of males (Fig. 2 and 3). As the number of males increased, the mother-to-offspring distance decreased, regardless the number of females (X^2, P<0.0001, n=2571 scans, Table 4). On the other hand, as the number of females increased, irrespective of the number of males, the mother-to-offspring distance was not significantly affected, even though there is a positive trend. Our interaction analysis shows that the number of adult females influences mother-to-offspring distance when the number of males is at its maximum observed (Fig 2, blue slope, and Fig 3, right graph) (X^2, P<0.01, n=2571 scans, Table 4). However, the number of males does not affect significantly the distance when the number of females is at its maximum observed.

Table 4 Intercept = distance. Parameter estimates, standard errors and p-values of the generalized mixed effect model: *Model1 <- lmer(dist ~ iage + moage + fem*male + dom + exper + soc + (1|Focal) + (1|Date), data=xdata, REML=F).* Left: males with quantitative data, right: males with binary data. Significant values are in bold.

Males as quantitative data (1 to 9)					Males as binary data (absent 0, present 1)				
	Estimate	Std. Error	z value	Pr(>|z|)		Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.095564	0.79594	-1.376		**Intercept**	0.350948	0.788406	0.445	
Infant age	0.935185	0.214429	**4.361**	**0.000197*** **	**Infant age**	0.946299	0.293396	**3.225**	**0.002095** **
Mother age	0.016547	0.015523	1.066	0.2924	**Mother age**	-0.003732	0.018481	-0.202	0.84
Nb of females	0.062784	0.043593	1.44	0.1505	**Nb of females**	-0.079457	0.126399	-0.629	0.5312
Nb of males	-0.224469	0.048432	**-4.635**	**3.785e-06 *** **	**Nb of males**	-0.052749	0.165990	-0.318	0.7513
Maternal rank	-0.006091	0.043456	-0.14	0.8887	**Maternal rank**	0.004708	0.163536	0.029	0.9771
Maternal experience	-0.076186	0.113882	-0.669	0.5039	**Maternal experience**	-0.020280	0.131459	-0.154	0.8776
Social experience	0.002609	0.016048	0.163	0.871	**Social experience**	-0.004017	0.014548	-0.276	0.7851
Male : Females	0.105873	0.034618	**3.058**	**0.002295** **	**Male : Females**	0.161270	0.155980	1.034	0.3062

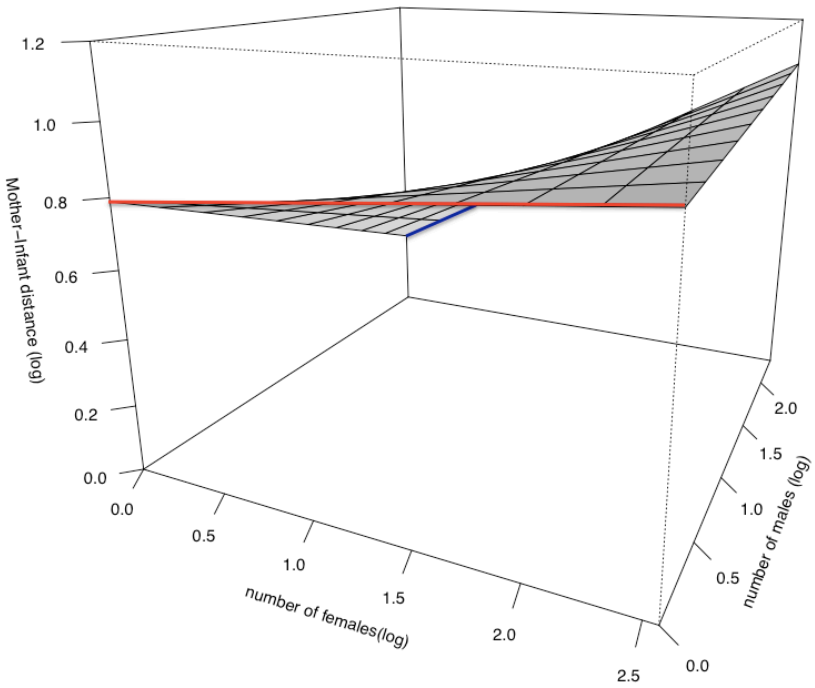

Figure 2 3D plot with males as quantitative data, showing the influence of the log10 number of adult and sub-adult males and females on the log10 mother-to-offspring distance (response variable). Red line (front) indicates when there are no males and the blue line (rear) indicates when the number of males is at its maximum observed. The blue slope is significant (p = 3.8e-6***) and maximum observation of individuals (mixed, rear right corner) is also significant (p = 0.0023**.

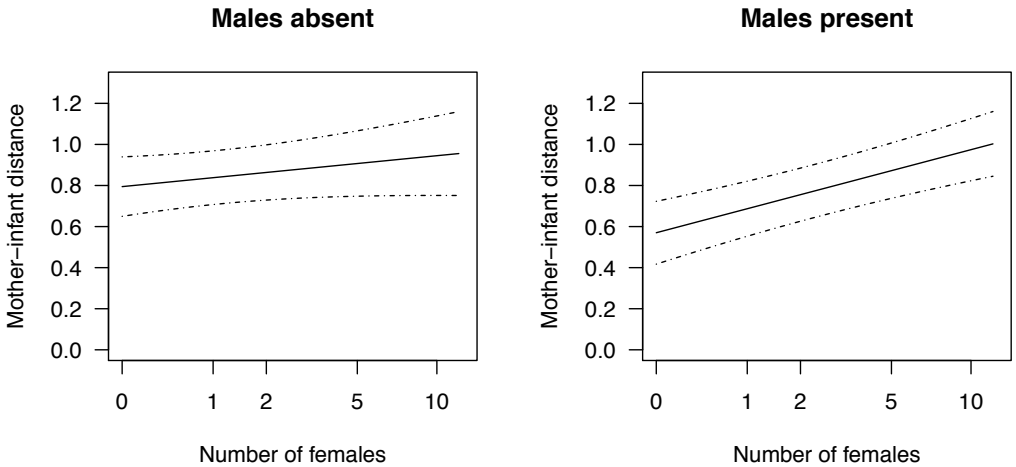

Figure 3 Graphs representing the log10 mother-to-offspring distance (response variable) as a function of the log10 number of adult females with males as binary data (left: males absent, right: males present). The effect is not significant, which is probably due to lack of variation in parties when there were only males with the focal mother (67% of time there was only the mother with one male).

Number of adult males and females vs proximity maintenance

For the proximity maintenance, that is the number of approaches made by the mothers towards their infant, the analysis confirms our prediction, namely: the increasing number, and the presence of adult males and females increases the number of approaches (Fig. 4 and 5). However, when a mother was alone with other males, results do not support our prediction. Indeed, with zero females present in the subgroup and the number of males increasing, the number of approaches made by the mother decreases (X^2, $P<0.01$, n=895 scans, Table 5).
Adult females only (with no males around) also, as expected, negatively affected the proximity maintenance. The more females present in the subgroup, the less a mother approached her infant (X^2, $P<0.01$, n=895 scans, Table 5). As for the mother-to-offspring distance, the mixed party composition affects significantly the spatial relationship – as a measure of approaches made by the mother – between mothers and their infants (X^2, $P<0.001$, n=895 scans, Table 5).

Table 5 Intercept = approaches made by the mother. Parameter estimates, standard errors and p-values of the generalized mixed effect model: *Model2 <- glmer(MoAp ~ iage + moage + fem*male + dom + exper + soc + (1|Focal) + (1|Date), family=binomial, data=app).* Left: males with quantitative data, right: males with binary data. Significant values are in bold.

Males as quantitative data (1 to 9)					Males as binary data (absent 0, present 1)				
	Estimate	Std. Error	z value	Pr(>|z|)		Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.00391	1.38488	-0.725		**Intercept**	-0.99643	1.32219	-0.754	
Infant age	0.05894	0.45858	0.129	0.897723	**Infant age**	0.04511	0.43244	0.104	0.916923
Mother age	-0.04054	0.03065	-1.323	0.185895	**Mother age**	-0.03643	0.02934	-1.242	0.214393
Nb of females	-0.91525	0.26125	**-3.503**	**0.000459 *****	**Nb of females**	-1.01913	0.27886	**-3.655**	**0.000258*****
Nb of males	-0.98941	0.33477	**-2.955**	**0.003122 ****	**Nb of males**	-1.92142	0.43299	**-4.438**	**9.10e-06 *****
Maternal rank	0.43879	0.27754	1.581	0.113876	**Maternal rank**	0.42174	0.26432	1.596	0.110587
Maternal experience	0.80734	0.21541	**3.748**	**0.000178 *****	**Maternal experience**	0.77550	0.20687	**3.749**	**0.000178*****
Social experience	-0.04462	0.02603	-1.715	0.086403	**Social experience**	-0.03874	0.02502	-1.548	0.121507
Male : Females	0.87018	0.20770	**4.190**	**2.79e-05 *****	**Male : Females**	1.71959	0.36193	**4.751**	**2.02e-06 *****

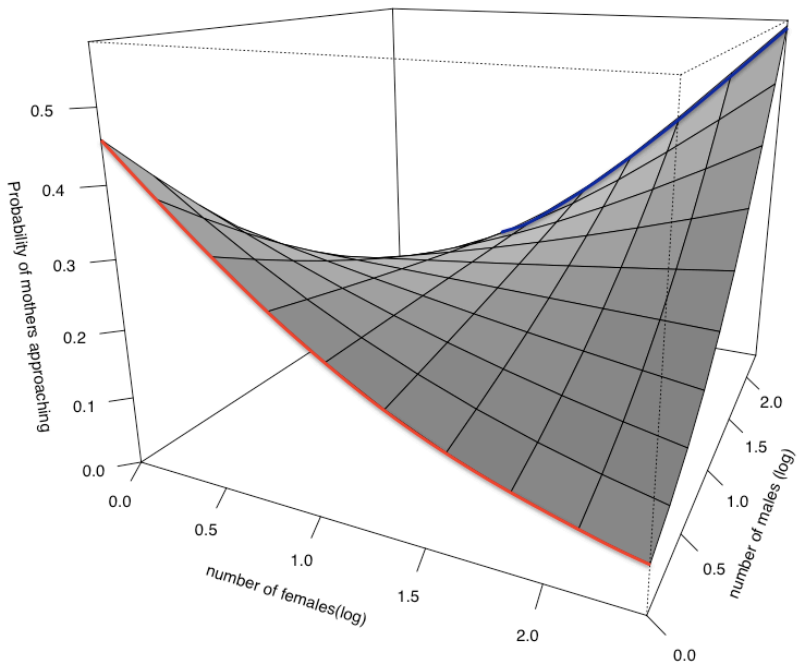

Figure 4 3D plot with males as quantitative data, showing the influence of the log10 number of adult males and adult females on the proximity maintenance, (response variable) defined as the probability of a mother approaching her infant. Red line (front) indicates when there are no males and the blue line (rear) indicates when the number of males is at its maximum observed. Both males and females alone had a negative effect on proximity (p = 0.003** and 0.0005***, respectively). Mixed parties had a positive effect (p = 2.8e-5***).

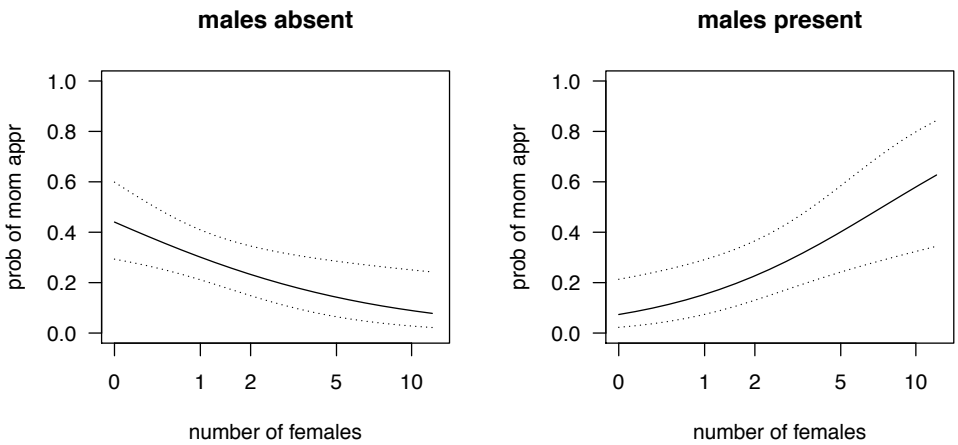

Figure 5 Probability of approaches made by mothers (response variable) as a function of the log10 number of adult females with males as binary data (left: males absent, right: males present). Strong effects are observable. The presence of males had a negative effect on proximity (p = 9.1e-6***), as the increasing number of females (p = 0.0003***). Mixed parties had a positive effect (p = 2.02e-6***).

Focal characteristics

Among all the predictors presented in Table 2, infant age had a significant effect and positive relationship with the mother-infant distance (X^2, $P<0.001$, n=2571 scans, Table 4). The older the infant gets, the bigger the distance is. However, the age of the infant did not affect the number of approaches made by the mother (Table 5).

Interestingly, the number of approaches by the mother was also influenced by other factors, but not the distance. There is no significant effect of maternal dominance rank but there is a tendency; the higher in the hierarchy, the less approaches towards their infant they made. The maternal social experience seems to have a non significant but not negligible effect in spatial relationships between a mother and her dependent offspring. Those who spent more time in the community tend to maintain proximity less than those who arrived more recently. Our results also show that more experienced mothers – successful mother with more offspring that reached 5 years of age – performed more approaches than less experienced females (X^2, $P<0.001$, n=895 scans, Table 5).

DISCUSSION

Mother chimpanzees with dependent offspring seem to adopt a well-defined strategy: spending less time in subgroups composed only by adult males and preferably joining mother or non-mother female parties. Surprisingly, the mothers also prefer to associate with mixed groups composed by both males and females rather than being alone. Our results show that mothers spent close to 70% of their time with mixed parties or female parties only, the latter being composed on average of 53% of other mothers. This might indicate a certain preference in maternal association patterns in staying with other mothers with dependent offspring. Other studies suggest that mothers with infants are less gregarious than non-mothers and/or males for different reasons (Chapman et al., 1995; Kappeler, 2000; Otali and Gilchrist, 2006; Trevathan, 1987). The scramble competition might be one of them (Kappeler, 2000). Chimpanzee diet relies mostly on ripe fruits, obtained from discrete and finite food patches. Thus, larger groups of individuals must visit more food patches. Mothers might prefer small parties because of the reduced travel costs (Chapman et al., 1995; Kappeler, 2000). More recently, Otali and Gilchrist (2006) proposed the infant safety hypothesis as an important reason explaining this discrepancies between mothers and males (Otali and Gilchrist, 2006).

The mother-infant spatial relationship is greatly influenced by the absence or presence of other community members. Mothers seem to adapt to each situation – here, party composition. With only males present in a 30-meter perimeter, the mother-to-offspring distance is reduced to the minimum (i.e. in contact), which, in turn, reduces proximity maintenance drastically. On the other hand, with only females, the distance is higher but the proximity maintenance reduces to nearly zero approaches made by the mother. Based on our results, it appears that the presence of males has an important influence on the distance but the presence of females seems to attenuate this influence. One reason for these observations might be that female-female aggressions are very rare and happen under very specific demographic or ecological circumstances (Otali and Gilchrist, 2006; Townsend et al., 2007). This low level of aggression among females might relax mothers and allow them to be less attentive towards their offspring. The infant can play with other infants and approach other individuals. Males, on the contrary, are more likely to threaten young individuals. Male chimpanzees are known for their violent behavior towards conspecifics (Trevathan, 1987; Wrangham and Peterson, 1996). Our results indicate a trend to reduce the distance with infants to protect them in case of sudden male

surge in aggressiveness. The more individuals there are in the party – maximum number of adult females and males observed – the higher is the distance to the infant and the more approaches a mother will do. When alone, mothers also keep a close distance to their offspring. This observed closer distance of mothers to their infants, while being alone in the family unite, compared to being in females or mixed groups, could be explained by the availability of time not spent in socializing with others.

However, results are not significant when males are taken as binary data (presence/absence). This could be explained by the fact that high number of males present with the focal mother was a rare event. When mothers were in male parties, the party consisted of only one other adult or sub-adult male during 67% of the time. Thus, data might not be sufficient to support the results from the quantitative males model.

Sonso mothers are more gregarious than mothers from another Ugandan community, the Kanyawara community (Otali and Gilchrist, 2006). In this community, where mother-to-offspring distance was also used as an index of maternal attention, the mothers spend more time alone or with females only. In the Sonso community, they spend one third of their time in bigger mixed parties. It has already been demonstrated that Sonso females were more gregarious than other East African chimpanzees (Thompson and Wrangham, 2006). The Sonso mother-to-offspring distance was higher in mixed parties than in any other party, and the maintenance of proximity was as well. The mothers seemed to control this distance. A reason for increased distance in male-female parties could be a “dilution effect”, a term often used in studies of vigilance for predators (Boesch, 1991; Noë and Bshary, 1997). In mixed parties, the female/male ratio was 1.1 female for 1 male. When more females are present, the chances of becoming a male’s target are smaller. This effect reduces individual risks of being attacked – by a predator or, here, a male conspecific, displaying for sexual or foraging reasons. Another reason for this less attentive maternal behavior might be a result of increased opportunities for socializing and for associating with a bond partner, which might increase chances of support if aggressed. It is interesting to note that it is only in the Sonso community that female coalitions against male aggressions have been observed, a strategy that may help reduce the severity and effectiveness of those aggressions (Newton-Fisher, 2006). Mothers might feel safer with females around, as they might get support if aggressed. However, this female behavior is very rare and Sonso males are known for their capacity of infanticide (Newton-Fisher, 1999). Ecological and demographic factors might be the reason why Sonso females are more gregarious and thus increase their opportunity for

coalitions. These associations are absent if females are essentially solitary (Newton-Fisher, 2006).

We confirm that infant age is a very important factor influencing mother-to-infant distance; the older the infant gets, the greater the distance between a mother and the infant is. These results could be linked to primate infant development. As they grow older, they become “leavers” instead of “approachers” (Altmann, 1980; Maestripieri et al., 2002). Also, offspring are more and more interested in other individuals and the environment and go more often on excursions, breaking and making contact on their own (Plooij, 1984). As soon as infant primates are able to move on their own, they leave their mothers to play with other young primates (Napier and Napier, 1994).

Regarding focal characteristics, we found that higher ranked mothers tended to maintain proximity less often than low ranking females. Dominance rank plays a big role for infant survival in many primate species (Pusey et al., 1997). Higher-ranking females may be less vulnerable to threats and more likely to get support from conspecifics if aggressed. Also, our results suggest a tendency for mothers who spent more time in the community to make less approaches towards their infants, showing less attention. These individuals might have had a longer time to form strong social bonds with other group members, thus reducing risks of aggression (Lehmann and Boesch, 2009). On the other hand, we found that experienced mothers maintained a higher proximity with their infant, and can be defined as more protective than younger, inexperienced mothers. Indeed, maternal protectiveness can be reflected by spatial relationships (Fairbanks, 1996). Mothers who make more approaches can be defined as more protective. Studies on variations in maternal style have provided several predictions based on the mother’s experience. One says that young, inexperienced mothers will put more efforts into maternal care because they are less competent (Fairbanks, 1996; De Lathouwers, 2004). The other one suggest that, following life-history changes in reproductive value, younger ones have more to lose in the future and will terminate investment on their infant earlier, while older, more experienced mothers would be unlikely to produce another infant (Pianka and Parker, 1975; De Lathouwers, 2004). These results show how infant social opportunities depend on maternal characteristics. An infant from a higher ranked mother could spend more time socializing with peers. The infant safety hypothesis and the infant integration hypothesis are both well influenced by maternal factors. The safety of an infant from a low ranked mother is more at risk, which in turn prevents the infant from socializing since the mother will keep him apart from conspecifics.

CONCLUSION

Mother-to-offspring spatial relationships are affected by maternal association patterns and some maternal identity characteristics such as her maternal experience. The rank of a mother within the community and her social experience – defined as the time since she was first seen in the community – both seem to play a role also. Longer fieldwork will be needed to confirm these possibilities. However, we have been able to address our main question. How mothers adapt to different party compositions? Males seem to be the main influence on maternal care and vigilance. Females, on the other hand, may allow mothers to feel safer from males. Our observations are compatible with the "infant safety" hypothesis and supports that early exposure of infants to other group members relies on the sociability of the mothers, which is linked to maternal association patterns and their experience as mothers (the "infant integration" hypothesis). Both the safety and the social integration of the infant are essential for its good cognitive and social development.

Understanding which factors influence mother-to-offspring behavior in different social situations and based on maternal experience and social status is necessary and important for primate research. Further research could study the link between maternal activity and party composition. Whether the mother is resting or foraging likely impacts on her relation with her offspring. Big and mixed parties may be associated with big fruiting trees. Thus, mother-to-offspring distance might be related to the diameter of a tree crown, regardless of party composition. Mother-offspring spatial relationships may vary in mixed groups because the mother is busy foraging, thus impeding her to keep an eye on her infant. How chimpanzee mothers behave probably depends on demographic and ecological factors that differ between communities. This is why this type of research should be extended to other groups and geographical areas.

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APPENDIX

MOTHERING STYLES IN THE WILD CHIMPANZEE *(Pan troglodytes schweinfurthii)* OF THE SONSO COMMUNITY AT BUDONGO FOREST, UGANDA

Abstract

Science has for long been interested in the effects of mother-offspring interactions on the social and cognitive development of primate infants. Studies confirmed that individual differences exist in the way a mother interacts with her infant. Based on the observation of a basic set of maternal behaviours, a terminology has been created distinguishing between "protective" mothers, "distant" mothers and "rejecting" mothers. This terminology expands through captive *Pan* species. I went to Uganda to collect mother-infant interaction behaviours, such as making contact, breaking contact, approaching, leaving, grooming, breast feeding, and play. My aim was to assess inter-individual differences in maternal styles in wild eastern chimpanzees using factor analysis, and then observe what factors influence these variations. The analysis shows weak strength and therefore, the results can not be used to answer the question. However, the factor analysis extracted three factors ("protectiveness", "rejection" and "distance") from nine basic maternal behaviours that explain 74% of the variance. Because any conclusions can be drawn, this paper is a descriptive work. Further research on the subject would need more data, and at different time ranges, to increase the strength of the factor analysis and to draw conclusions.

INTRODUCTION

Extensive studies of mother-infant relationships in nonhuman primates have revealed that mothers play one of the most important, if not primary, role in the social and cognitive development of the infants (Bardi and Huffman, 2002, 2006; De Lathouwers and Van Elsacker, 2004; Fairbanks and McGuire, 1988). Consequently, parental care, here maternal care, might have a direct effect on an individual's future reproductive success (Clutton-Brock, 1991; Otali and Gilchrist, 2006). This is where differences in maternal care and behaviors between mothers are interesting, as differences in maternal styles might lead to different development and fitness in the offspring.

Early studies in the 1960s and 1970s on captive and wild primates confirmed individual differences in the way primate mothers treat their infants (Fairbanks, 1996). Some mothers were consistently more restrictive towards their infant's attempt to move out of contact, while other mothers showed more rejecting or inattentive behaviors (Altmann, 1980; Fairbanks, 1996). As reviewed by Fairbanks, Hinde and his colleagues established a standard set of behaviors and observational methods that are now globally adopted to describe mother-infant interactions. This set of behaviors includes: time spent in contact, making contact, approaching, breaking contact, leaving, rejecting, restraining and grooming (see Fairbanks, 1996).

Factor analyses, which reduce the number of maternal behavioral variables and detect the structure in the relationship between them is the analytical tool that is the most used in this area of research (De Lathouwers and Van Elsacker, 2004). To reflect differences in mothering style, a terminology has been created that expands maternal behavior to two dimensions (Bardi and Huffman, 2002; Fairbanks, 1996). The "protectiveness" factor describes mothers that initiate contacts, approach, restrain and groom their infant more often than individuals belonging to the "rejection" factor. This one is positively correlated with mothers who break contacts, leave and reject their infants more often (Bardi and Huffman, 2002).

Until recently, most studies on primate maternal styles have been conducted on *Cercopithecine* species, like Japanese macaques and Vervet monkeys (Bardi and Huffman, 2002; Fairbanks and McGuire, 1988; Schino et al., 1995) and all those studies show a high degree of consistency in the two basic dimensions of maternal behavior.

De Lathouwers and Van Elsacker tested the exploratory factor analysis method on 8 captive mother-infant pairs of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), to determine whether or not it works in higher taxa. Results showed similarities in the pattern of "protectiveness" between *Pan* and *Cercopithecine* species. However, the "rejection" dimension is found to be divided into two separate factors, "distance" and "refuse" (De Lathouwers and Van Elsacker, 2004).

To my knowledge, this approach has never been tested on wild mother-infant pairs of chimpanzees. Thus, my aim was to use the same methods (exploratory factor analysis) in order to assess potential inter-individual differences in maternal styles in wild eastern chimpanzees (*Pan troglodytes schweinfurthii*). If there is a difference in mothering styles between mothers, what are the factors that influence these dissimilarities?

METHODS

The subjects are 10 mother-infant pairs of wild eastern chimpanzees (*Pan troglodytes* schweinfurthii) of the Sonso community. The sample included 8 male and 2 female infants. At the beginning of the study, estimated maternal age ranged from 19 to 41 years and infant age ranged from 8 to 76 months. The study was conducted between July 2016 and December 2016 in BCFS, Uganda. We did all day follows on the mother-offspring pair noting down general behaviours like resting, foraging, grooming and specific mother-offspring interactions in a one-zero method (Altmann, 1974). Mother-offspring interactions consisted of making contact, breaking contact, approaching, leaving, restraining, rejecting, grooming, breast-feeding and play. Making contact, breaking contact, approaching and leaving were collected both for the mother and the infant. Behaviours such as breast-feeding or grooming are an underestimation, since it is quasi-impossible to observe all events in the wild.

For factors influencing a potential inter-individual variability in mothering styles, we collected data on focal characteristics, such as infant age, maternal age, maternal rank and maternal experience – number of infants that were successfully reared until 5 years of age (De Lathouwers, 2003).

We used factor analysis, with varimax rotation, to extract and interpret the components revealed by principal component analysis on the nine mother-offspring variables. Factor loadings were then calculated. To know the number of factors to extract, the Kaiser-Guttman "eigenvalues greater than one" was applied. ANOVAs were performed to determine what factors influence maternal styles. Linear model was used, with the response variables being the three dimensions extracted by the factor analysis: "protectiveness", "rejection" and "distance". Predictor variables included infant age, maternal age, maternal rank and maternal experience. All test were two-tailed with significance level $P<0.05$. Data were analyzed using the package lme4 in R 3.3.2 with RStudio 1.0.136.

RESULTS

From the nine variables, the factor analysis extracted three significant components, for a total retention of 74% of the total variance (Table 1). The percentage of variance that is explained by each component and in total is indicated.

Table 1 Extraction of significant components

Factor	Eigenvalue	% total variance
1	2.59	28.8
2	2.23	24.7
3	1.85	20.5
Cumulative %		74

Three factors retained by factor analysis using the "eigenvalue greater than one rule for the nine mother-infant behaviours. The percentage of variance explained by each component and in total is indicated.

Table 2 includes the factor loadings for each variable. The first factor explains 28.8 % of the total variance. This factor can be assimilated to the "protectiveness" dimension already proposed by several studies, as it correlates positively with "grooming", "breast-feeding", "restraining" and "play". Factor number 2 explains 24.7% of the total variance. It can refer to the "distance" dimension, since it correlates with "making contact", "approaching" and "
leaving". The third and last significant factor refers to the "rejection" dimension, or "refuse". It is associated with "breaking contact" and "rejection".

Table 2 Factor loadings showing a matrix of correlation between maternal behaviours and the three factors extracted by factor analysis.

Maternal behavior	Protectiveness	Distance	Refuse
Making contact	0.18	**0.47**	0.21
Breaking contact	0.18	0.54	**0.72**
Approaching	-0.42	**-0.76**	-0.12
Leaving	-0.39	**0.92**	
Grooming	**0.58**	0.27	0.16
Rejecting	-0.2		**0.98**
Restraining	**0.71**		
Breast feeding	**0.6**	0.48	0.52
Play	**0.98**		

None of the ANOVAs testing for causes of inter-individual differences were significant. Only tendencies were assessed for the "protectiveness" and "distance" dimensions. "Protectiveness" seems to be negatively correlated with infant age (P=0.05) (Fig. 1) and the factor scores on "distance" follow a negative relationship with maternal experience (P=0.06, NS) (Fig. 2).

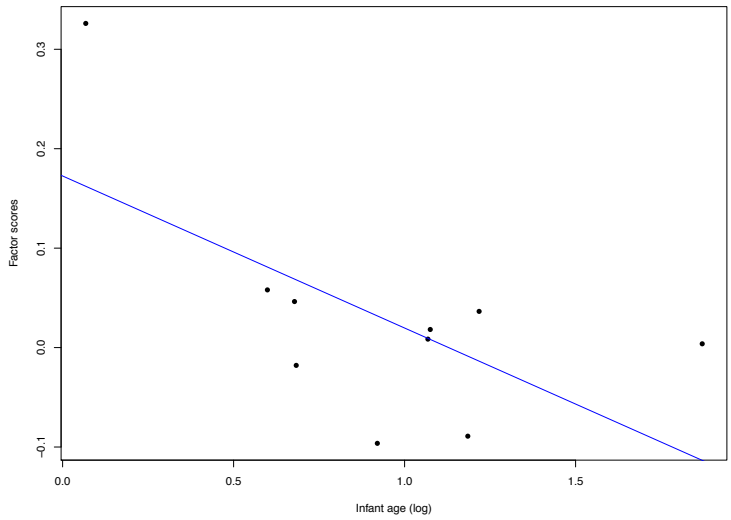

Figure 1 Factor scores on "protectiveness" according to infant age (log). There is a negative tendency between infant age and protective behaviours by mothers. Mothers seem to be less protective when the infant gets older.

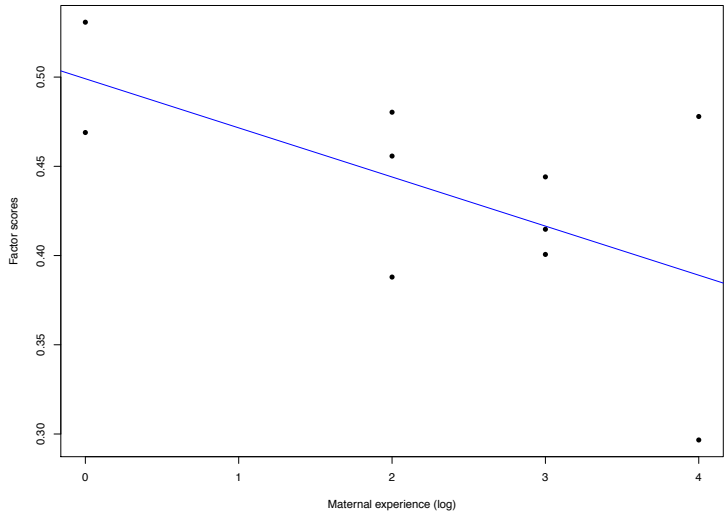

Figure 2 Factor scores on "distance" according to maternal experience (log). No significant effect. There is a negative trend between maternal experience and the "distance" dimension. The more experience a mother has, the less contacts she will make.

DISCUSSION

The aim of this study is to investigate whether factor analysis used to determine maternal styles in *Cercopithecine* species and captive chimpanzees can be applied to wild chimpanzees. Furthermore, if factor analysis is successful, we want to determine what factors influence differences in maternal styles. It is important to note that it is a descriptive study, and not an analytic one.

The results show interesting similarities with previous studies. We also found three extracted factors from the factor analysis, namely "protectiveness", "rejection" and "distance". However, their interpretation might be different, since not all the same maternal behaviours as Fairbanks

(1996) and De Lathouwers (2004) were collected during the fieldwork. Conditions in captivity and in the wild differ in their consistency, visibility and efficiency of data collection. Behaviours such as mothers rejecting the infants approaching or restraining their infants leaving were very rarely observed in the wild. The interpretation of the extracted factors has to be taken very carefully. The factor analysis shows very weak statistical strength. The modification of one variable or the removal of one focal changes the entire factor loadings, giving the possibility for other interpretations. Therefore, we cannot interpret the results at all. The first factor, that we termed "protectiveness", correlates with every mother-infant interaction that needs contact; namely grooming, breast-feeding, restraining and play. The second factor, named "distance", refers to the spatial relationship between a mother and her infant, which is making contact, approaching and leaving. These mothers could be described as laissez-faire mothers. The third factor, "refuse", correlates with breaking contact and rejection. This type of maternal style indicates rejecting mothers.

The second aim of this study was to determine which factors affect maternal style. Here again, we cannot conclude anything from these results, since the differences in factor scores from the factor analysis have been tested with ANOVAs. No significant results were found, only tendencies.

CONCLUDING REMARKS

It is important to be sure about the aim of the study. Is the goal of the study to compare the results with previous studies, or is it to show a method can work in different conditions, for different variables? In this study, it was not very clear. To test the question of maternal styles using the method proposed in earlier papers, I should have had collected the exact same mother-infant interaction behaviours. I show that factor analysis is possible with wild species, but longer and more consistent work is needed.

Further research would need to collect more data in order to define maternal styles in wild chimpanzees since the methods used need a certain amount of observation of all the integrated behaviours. Also, some of these behaviours (*i.e.* rejection) are very rarely observed in wild communities and the conditions are harder. Thus, a solution would be to design the study differently and exclude some behaviours while including other ones.

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