Durability and flexibility of chimpanzee grooming patterns during a period of dominance instability

Nicola F. Koyama[1], Kirsty Ronkainen[1,2] and Filippo Aureli[1,3]

[1]Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, United Kingdom

[2]Berkshire College of Agriculture, United Kingdom

[3]Instituto de Neuroetologia, Universidad Veracruzana, México

Short title: Grooming patterns during instability

Corresponding author:
Nicola F. Koyama
Research Centre in Evolutionary Anthropology and Palaeoecology
Liverpool John Moores University
Byrom Street
Liverpool L3 3AF
United Kingdom
n.f.koyama@ljmu.ac.uk
+44 1512312627

ABSTRACT

Growing evidence from studies on primates and other taxa has shown that the maintenance of long-term affiliative patterns influences fitness. Thus, understanding how individuals regulate social interactions in response to environmental and social factors contributes to our understanding of the evolutionary basis of sociality. We investigated the durability of affiliation patterns in chimpanzees across three 3-month periods of varying social uncertainty depending on the degree of stability in the male hierarchy, with a 2-yr gap between each period. Periods were unstable (no clear alpha male), recently stable (new alpha male just established) and stable (alpha male in place for two years). We focused on three features of social exchange shared by human and non-human primates: consistency of exchanges across periods, durability of preferred partners, and degree of reciprocity in each period. We compared male-to-male, female-to-female, male-to-female and female-to-male grooming patterns. Overall, more grooming was exchanged in the stable period. Grooming patterns were not consistent across the three periods, but were only consistent between the recently stable and stable periods for female-to-female and male-to-female dyads. As predicted from the opportunistic nature of male relationships, male-to-male grooming was least likely to be correlated across all periods and males had relatively fewer durable (i.e., preferred partners in all periods) same-sex partners than females. Our predictions that grooming reciprocity would be less likely during the unstable period and in male-male dyads were only partially supported. We found grooming reciprocity in all periods for female-female dyads but only in the stable period for male-male and female-male dyads. Although long-term affiliative patterns are well studied in primates, this is the first study to investigate the association between social uncertainty and durability of affiliative patterns.

Our findings suggest social uncertainty influences social exchange and highlight the importance of considering group instability in studies of social relationships.

Key words: social uncertainty; exchange; long-term; primate

INTRODUCTION

Recently, empirical research demonstrating a direct link between social relationships and fitness has been accumulating across a range of taxa, e.g. primates (Lehmann et al., 2016; Schülke et al., 2010; Silk et al., 2003, 2009), horses (Cameron et al., 2009), dolphins (Stanton & Mann 2012), rodents (Wey et al., 2013), and birds (Royle et al., 2012). Therefore, investigating how individuals manage their social relationships in response to environmental and social factors can shed light on the evolutionary basis of sociality (e.g. Dunbar & Shultz, 2010; Kutsukake 2009). Long-term studies are recognized as providing a wealth of data for a variety of analyses (Kappeler & Watts, 2012). For example, long-term data have provided the opportunity to focus on affiliation patterns over time. Among non-human primates the most frequently used measures of affiliation are spatial proximity and grooming exchanges between group members (Cords, 1997; Dunbar, 1991). Using these measures, long-lasting affiliation patterns have been documented in several non-human primate species, such as baboons (*Papio sp.*, e.g. Silk et al., 2006; 2010; 2012), rhesus macaques (*Macaca mulatta*, Weinstein & Capitanio, 2012; Massen & Sterck, 2013), Japanese macaques (*M. fuscata*, Nakamichi & Yamada, 2007) and bonobos (*Pan paniscus*, Moscovice et al., 2017). Changes in group membership, and thus partner availability, can create social instability (e.g. Beisner et al., 2015) which has been shown to have negative health consequences e.g. in rodents (*Rattus norvegicus*, Herzog et al., 2009; *Heterocephalus glaber*: Clarke & Faulkes 1997) and primates (*M. mulatta*, Capitanio & Cole 2015; *M. fascicularis*, Manuck et al., 1983). Two earlier studies have explored the effect of rank reversals in the male hierarchy on relationships within a primate group (de Waal 1989; Perry 1998) but none so far have explicitly considered the impact of social uncertainty on the durability of affiliation patterns in non-human primates, and the role of social uncertainty on durability of human social relationships is poorly understood (Bukowski et al., 1998). Chimpanzees (*Pan troglodytes*) are a suitable species to examine the role of social uncertainty on the durability of affiliation patterns as enduring affiliation patterns have been reported between males and between females (Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009; Koski et al., 2012; Mitani, 2009), and males are known to engage in flexible social interactions which may depend on social uncertainty (e.g. Nishida, 1983).

Affiliation between male chimpanzees is high both in the wild and in captivity (reviewed in Muller & Mitani, 2005). Males are the philopatric sex, are more gregarious and spend more time grooming one another than females do (e.g. Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1979). Previous research has emphasized the opportunistic nature of male-male social interactions (e.g. Nishida, 1983; de Waal, 1989; Newton-Fisher, 2002), however, affiliation patterns in some male-male dyads have been found to be durable for up to 10 years in the wild (Mitani, 2009).

Chimpanzee females have been often described as having weak social relationships with one another due to their dispersal from the natal group limiting opportunities to interact with kin, and the lack of a need to form coalitions (Nishida, 1979; Goodall, 1986;

Wrangham, et al., 1992; Arnold & Whiten 2003). However, more recent findings reveal that females can form long-term cooperative relationships and opportunistic female-female coalitions (Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2006; Lehmann and Boesch, 2008, 2009; Langergraber et al., 2009; Wakefield, 2013; Foerster et al., 2015). The potential for female chimpanzees to form strong relationships was first documented in captivity (de Waal 1984, 1989; Baker & Smuts, 1994), and subsequent captive studies have continued to provide evidence that females can form high-quality relationships with each other (e.g. Fraser et al., 2008; Koski et al., 2012). Only one study so far has assessed temporal durability in female grooming patterns (Lehmann & Boesch, 2009). While the majority of females had at least one same preferred association partner (association being defined as being in the same subgroup) for three of four consecutive years, only a fifth of all adult females maintained a long-term female grooming partner and only 5% of dyads were classified as long-term grooming partners.

Fewer studies have focused on affiliative exchanges between females and males in chimpanzees. In the wild levels of proximity and grooming are lower in female-male dyads than in male-male dyads but higher than in female-female dyads (Langergraber et al., 2013; Machanda et al., 2013). In captivity, there appears to be less variation in affiliation between dyads of different sex-combinations (Fraser et al 2008). Both wild and captive studies report that females form coalitions with males (de Waal, 1994; Kahlenberg et al., 2008). There is also some evidence that interaction patterns between females and males are maintained across time as indices of female-male association in the same subgroup during two periods three years apart were highly correlated (Langergraber et al., 2013).

Thus, there is growing evidence for the existence of durable affiliation patterns between males, between females and between females and males, but no study so far has examined the impact of social uncertainty on the durability of grooming patterns. Gilby & Wrangham (2008) compared association preferences between periods with different alpha males, but omitted the replacement period from their analyses. Two studies have examined how affiliation patterns vary depending on social instability but they did not compare the consistency of dyadic affiliation patterns across periods differing in social uncertainty (de Waal, 1984; Hemelrijk & Ek, 1991).

The gradual change in alpha male that began at the start of our study provided a unique opportunity to investigate how social uncertainty affected the durability of affiliation patterns in chimpanzees. We identified three periods of varying social uncertainty depending on the degree of stability in the male hierarchy (unstable, recently stable and stable) spanning four years. We focused on three features of social exchange that are shared by human and non-human primates (e.g. Krappman, 1998; Massen, et al., 2010; Silk, 2002; Vigil, 2007): the consistency of exchanges across periods, the durability of preferred partners and the degree of reciprocity in each period.

We examined these three features by investigating grooming exchanges in male-male, female-female and female-male dyads. If social relationships were not affected by social uncertainty, we expected grooming to be exchanged consistently over time and therefore be correlated across the three periods (Prediction 1). If grooming exchanges were disrupted by the lack of a clear alpha male, we expected consistency only between the recently stable and stable periods (Prediction 2). Due to the opportunistic nature of male-male relationships, especially during periods of uncertainty such as dominance instability, we expected male-male grooming patterns to be the least likely to be correlated across all periods (Prediction 3). We also expected differences in the durability of preferred grooming partners, with a relatively smaller number of preferred partners maintained across all three periods for male-male dyads than for female-female and female-male dyads (Prediction 4). Similarly, we expected grooming reciprocity to be less likely during the unstable period (Prediction 5). This pattern is expected especially for male-male dyads (Prediction 6), as males are expected to shift their exchange of grooming for grooming to grooming for potential support during unstable periods when alliances may be shifting.

METHODS

Subjects and housing

The study group was well established and consisted of 20 adults (5 males and 13 females), two adolescent females and nine immature individuals. Females were considered as adult after they were observed with sexual swellings and mating with males. Adult males were between the ages of 25 and 34 years at the start of the study but we also include M1, who was 13.5 years old in this age category due to his successful challenge for the alpha male position. All five adult males and 12 adult females (one female aged 53years that never groomed was excluded) were selected as subjects. Using pedigrees, we considered as kin those maternally related individuals with $0.125 \leq r \leq 0.5$. A total of seven kin adult dyads (one male-male, one female-male and five female-female dyads) were present in the group.

The group was housed at Chester Zoo, UK in an enclosure containing a 143-m², 12-m high round indoor yard, and a 2000-m² outdoor area covered in grass (Caws et al., 2008).

The outdoor area contained a variety of bushes and shrubs and 50 vertical poles with interconnecting ropes and nets for enrichment purposes whilst the indoor enclosure contained a 9m high complex metal tower with platforms, ropes and nets and an artificial termite-fishing area. The chimpanzees had access to these two areas during the day and an off-show area during the night. Water was freely available indoors and outdoors, nesting material was provided daily and the chimpanzees were fed 2-3 times a day on fruit, vegetables and pellets.

In 2000 the incoming alpha male (M1) ceased to greet the outgoing alpha male (M2) with pant-grunts, the typical submissive signal in chimpanzees (Noë et al., 1980). This was the start of a gradual rank reversal (or inside takeover) process (Teichroeb & Jack, 2017) until M1 was established by the end of 2002 (Wehnelt et al., 2006). From September 2002, the remaining males consistently greeted with pant-grunts the new and not the former alpha, and female pant-grunt greetings switched to be given at a higher rate to the new rather than former alpha. Based on the consistency and rate of pant-grunts among adult males, we labeled the 2000 period with an unclear alpha male as the unstable period; the 2002 period with the recent settlement of the alpha male dispute as the recently stable period; and the 2004 period with a clear alpha male for at least two years as the stable period. Of the remaining three males only one male could be clearly and consistently positioned at the bottom of the hierarchy (M5) and the remaining two males were ranked equally (M3 and 4) as no pant-grunt greeting was observed between them. It was not possible to construct a dominance hierarchy for females due to the scarcity of dominance-related interactions between females.

Data collection

Observations were collected by a trained research assistant and KR in three periods from October to December in 2000, 2002 and 2004 on weekdays between 10.00 and 16.00. The research assistant trained KR to ensure inter-observer reliability. Instantaneous scan sampling with a minimum of 15-minute intervals was carried out on each subject to record the identity of grooming partners and whether grooming was given or received. As in some previous studies (e.g. Lehmann & Boesch, 2009) mutual grooming was recorded as two separate grooming events (i.e. A grooms B and B grooms A).

Statistical analyses

As females' attractiveness can influence grooming interactions with males (e.g. Anderson et al., 2006; Koyama et al., 2012; Mastumoto-Oda et al., 1998; Slater et al., 2008) we analyzed data from females when they did not have the ano-genital area swollen, i.e. not sexually attractive to males. There were days in which some individuals were not in the group, resulting in an uneven number of scans across dyads. The range of scans per dyad was 306-339 in the unstable period, 335-381 in the recently stable period, and 284-315 scans in the stable period. First, we tested for differences in the percentage of scans spent grooming between periods at the individual level with a repeated measures ANOVA, with Dunn-Šidák-corrected pair-wise comparisons, for each dyad type (female-female, male-male, male-female and female-male). Then, we constructed matrices of the percentage of scans spent grooming given (and of grooming received) for each dyad type for each period and carried out Kendall's ($\boldsymbol{\tau}_{rw}$) rowwise matrix correlation tests (de Vries, 1993, Hemelrijk et al., 1990), a variant of the Mantel test (Mantel, 1967), using Matman^{TM}

1.1 (de Vries et al., 1993). Matrix correlation methods avoid problems arising from the non-independence of dyadic data as the same individuals are present in multiple dyads and have been used widely in previous studies in chimpanzees (de Waal & Luttrell, 1988; Langergraber et al, 2009; Newton-Fisher & Lee, 2011; Stumpf & Boesch, 2010; Wakefield, 2013). Kendall's ($\boldsymbol{\tau}_{rw}$) rowwise matrix correlation test accounts for the presence of individuals in more than one dyad by running the correlations within rows.

To find out if grooming exchanges were consistent across the three periods (Prediction 1-2) depending on the dyadic sex combination (Prediction 3), we ran Kendall's ($\boldsymbol{\tau}_{rw}$) rowwise matrix correlation tests of grooming given between the unstable and the recently stable period, between the recently stable and the stable period and between the unstable and the stable period, for male to male grooming, male to female grooming and female to male grooming. As five of the total 66 female-female dyads (8 females) included close kin we used partial matrix correlation tests ($\boldsymbol{\tau}_{rw;XY.Z}$) that controlled for the effect of kinship while the correlation between grooming in the two years was calculated. We did not control for proximity across dyads as in captivity group members are always relatively close to one another, in contrast to the fluid party membership seen in the wild (Goodall, 1986; Nishida, 1979).

We ran 10,000 iterations for each rowwise matrix correlation test and report exact two-tailed p values, adjusting our level of significance using the sequential Bonferroni technique (Holm, 1979) to reduce the likelihood of Type 1 errors. As there were separate matrices for each dyadic sex combination (female-female, male-male, female-male and male-female) we treated each combination as a subset of *k* tests for the Bonferroni correction.

We evaluated the durability of preferred grooming partners depending on the dyadic sex combination (Prediction 4) by identifying the preferred grooming partners as those that were groomed above an individual’s dyadic mean in each of the three periods: unstable, recently stable and stable. Durable preferred grooming partners were those individuals that were preferred grooming partners in all periods.

To assess patterns of reciprocity (Prediction 5-6) based on partner choice (Schino & Aureli, 2017) across dyads within each period, we correlated grooming given matrices with grooming received matrices for each sex combination of dyads, partialling out kinship for the female-female dyads. In addition, to examine whether subjects exchanged grooming bouts more reciprocally with durable preferred grooming partners than with other grooming partners, we calculated a reciprocity index (Mitani, 2009 rescaled from Nishida, 1988) for each dyad:

$$1 – [g_{AB}/(g_{AB} + g_{BA}) - g_{BA}/(g_{AB} + g_{BA})]$$

where g_{AB} is the percentage of scans A spent grooming B, g_{BA} is the percentage of scans B spent grooming A. We calculated a mean reciprocity index for each individual with its durable preferred grooming partners and the remaining grooming partners for each period. We used a paired t-test to investigate differences between these mean reciprocity indexes at the individual level for females only, due to sample size constraints. We used SPSS 20.0 (SPSS Inc., Chicago, IL, U.S.A.) to analyze differences between periods.

At the time of the study, observational, noninvasive animal research did not require approval of the university ethics committee. The study adhered to U.K. legislation and to the American Society of Primatologists' Principles for the Ethical Treatment of

Primates. Chester Zoo approved the research protocols used in this study and gave permission to conduct the study.

RESULTS

Female-female grooming patterns

Grooming was observed in around two-thirds of all dyads in each period (Table 1). Females groomed other females differently across the three periods ($F_{2,22}=47.4$, $P<0.001$, with a higher percentage of scans spent grooming in the stable period (mean±SD: 7.3±2.7) than in the unstable (2.1±1.2; $P<0.001$) and recently stable period (1.9±1.1; $P<0.001$). There was no difference between the unstable and recently stable period ($P=0.9$).

Table 1 here

Consistency across periods. Female-female grooming patterns showed some consistency over the four years (Table 2) with positive correlations between the unstable and recently stable periods and between the recently stable and stable periods. However, there was no correlation between the unstable period and the stable period (Table 2), indicating an overall shift in grooming patterns over time.

Table 2 here

Durable preferred grooming partners. In each period the majority of females groomed a selected number of preferred partners but they groomed an even smaller number of preferred partners in all three periods (Table 3). Nine of 12 females had at least one durable preferred grooming partner, i.e. the same preferred partner in each of the three periods. Of the three females without durable preferred partners, one did not groom any other females in two of the three periods and two groomed preferred partners consistently in only two of the three periods. Six of the nine females with durable preferred partners had kin in the group, but two females with kin in the group did not have durable preferred partners. When we excluded kin, six of the 12 females had at least one durable non-kin preferred grooming partner.

Reciprocity. Grooming given and received within each period was positively correlated indicating grooming reciprocity (Table 2). The mean (±SD) reciprocity index with durable preferred partners was not significantly higher than that with other grooming partners in the unstable (durable= 0.36±0.2, other= 0.17±0.2; T_5=1.37, P=0.23) and recently stable (durable= 0.57±0.29, other= 0.33±0.23, T_8=1.7, P=0.14) periods, and not significantly different in the stable period, although close to the alpha level (durable= 0.84±0.16, other= 0.70±0.18, T_8=2.3, P=0.054).

Table 3 here

Male-male grooming patterns

Males groomed other males differently across periods ($F_{2,8}$=7.6, P=0.014), with a higher percentage of scans spent grooming in the stable period (3.4±2.1) than in the recently stable period (1.2±0.9; P=0.048). There was no difference between the unstable period (1.4 ±0.9) and the recently stable (p=0.9) or stable (P=0.2) periods.

Consistency across periods. Grooming given by males to other males was not overall consistent across the three periods, although there was a correlation in grooming given between the unstable period and the recently stable period (Table 4).

Durable preferred grooming partners. Three of the five males had at least one durable preferred grooming partner (Table 3); the durable preferred grooming partners were all non-kin. These three males were the new alpha male M1, M4 and M5.

Reciprocity. Reciprocity of grooming given and received was only found in the stable period (Table4).

Table 4 here

Grooming patterns between the sexes

Females groomed males differently across the three periods ($F_{1.3,14.3}$=15.0, P<0.001), with a higher percentage of scans spent grooming in the stable period (4.4±2.9)) than in the unstable (1.5±1.4; P=0.008) and recently stable period (1.1±0.7; P=0.004). There was no difference between the unstable and recently stable period (P=0.6). There was no difference in the percentage of scans spent by males grooming females among the three periods (unstable: 5.0±4.4; recently stable: 3.7 ±1.8; stable: 7.7±2.7; $F_{1,4}$=2.1, P=0.2).

Consistency across periods. There was some consistency in male grooming given to females across the three periods (Table 5). Males who groomed females in one period were more likely to groom them in the next period although these relationships shifted over the course of the study from the unstable to the stable period. There was a correlation in female grooming given to males only between the unstable period and the recently stable period (Table 5).

Table 5 here

Durable preferred grooming partners. Four of the five males had at least one durable preferred female partner across the three periods (Table 3). The new alpha male, M1 , preferentially groomed three female (non-kin) partners across all periods. The outgoing alpha male, M2, and M4 had two females as durable preferred partners, whereas M3 had only one durable preferred female partner. The lowest ranking male, M5, did not have any durable preferred female partner.

In contrast, only five of the 12 females had durable preferred non-kin male grooming partners (Table 3): two females had one durable preferred male partner (the outgoing alpha M2) and three females had two durable preferred male partners (M2 and M3 for one female and M3 and M4 for two females). None of the females had the new alpha male M1 or the lowest ranking male M5 as a long-term preferred male grooming partner.

Reciprocity. Similar to the male-male dyads, reciprocity of grooming given and received in male-female dyads only occurred in the stable period (Table 3).

DISCUSSION

We examined six predictions about how social uncertainty may affect the durability of affiliation patterns in chimpanzees by focusing on three features of social exchange: the consistency of exchanges across time, the durability of preferred partners and the degree of reciprocity. We did so by comparing grooming exchanges in male-male, female-female and female-male dyads across three periods differing in social uncertainty based on the degree of stability in the male dominance hierarchy. Prediction 1, that grooming was exchanged consistently over time, was not supported as no dyad type showed a correlation between the unstable and the stable period which were 4 years apart. Prediction 2, that consistency in grooming patterns occurred only between the recently stable and stable periods, was partially supported. A correlation between these two periods was found only for females grooming other females and males grooming females, but not for males grooming other males and females grooming males. Prediction 3, that male-to-male grooming was the least likely to be correlated across all periods, was overall supported, although female-to-male grooming was correlated only between two periods. Prediction 4 was supported as the number of preferred partners maintained across all three periods was relatively smaller for male-male dyads than for female-female and female-male dyads. Interestingly, within the female-male dyads the number of such preferred partners was relatively higher for males grooming females than for females grooming males. Prediction 5, that grooming reciprocity was less likely during the unstable period, was partially supported because there was reciprocity in female-female dyads during this period, whereas there was no reciprocity in the other dyad types during the unstable and the recently stable periods. Prediction 6, that grooming reciprocity was less likely during unstable periods in male-male dyads than in the other dyad types, was not fully supported as reciprocity was demonstrated in all periods in female-female dyads, but reciprocity could be shown only in the stable period in female-male dyads, like in male-male dyads. Overall, our findings support previous studies, as the majority of individuals appeared to maintain at least one durable partner, and add to a growing body of research on the durability of affiliation patterns in primates (e.g. Massen & Sterck, 2013; Mitani, 2009; Moscovice et al., 2017; Silk et al., 2010, 2012).

Similar to recent studies from the wild (e.g. Lehmann & Boesch, 2009; Foerster et al., 2015) and captivity (e.g. Fraser et al., 2008; Koski et al., 2012) we found evidence for durability of grooming patterns between chimpanzee females. They showed consistency between adjacent periods, but females shifted partner preferences between the unstable and stable periods, which were 4 years apart. This shift provides evidence for flexibility in female-female grooming patterns depending on changes in male dominance hierarchy. As chimpanzee females may be less sociable when they have a young infant (e.g. Otali & Gilchrist, 2006), one could argue that our findings may due to differences in the number of females with a young infant across periods. In our study, there was only one female with an infant in the unstable period and two females with an infant in the stable period. Contrary to what expected based on infant presence, we found more female grooming in the stable period than in the other two periods. All but one of the females maintained at least one preferred partner across all three periods, indicating resilience of some relationships through periods of dominance instability and social uncertainty. These durable preferred partners were kin and non-kin, and some females with female kin in the group had non-kin as durable preferred grooming partners.

There was overall little evidence for durability in females grooming males. We found only a correlation between the unstable and the recently unstable period. Only five of the 12 females had durable preferred male grooming partners. Interestingly, these partners were the outgoing alpha male and the middle ranking males, and no female preferentially groomed the new alpha male across periods. Female support for the outgoing alpha male has been previously reported; however, such support was later transferred to the new alpha male, highlighting the flexibility in females' relationships with males (de Waal, 1986). In our study, the durability of female preferences for male partners across periods of male dominance instability may be related to the gradual process of changing the alpha male. Similarly, the lack of a correlation between the unstable and stable period supports the flexibility in females grooming males.

Few studies have examined males' affiliation patterns with females with somewhat contrasting results (Langergraber et al., 2013; Machanda et al., 2013). Similar to the grooming patterns between females, we found males showing consistency in grooming females between adjacent periods. All males, except the lowest ranking male, had durable preferred female grooming partners, highlighting the importance of females as long-term partners for males. These findings support the observations of females playing an important role in mediating male-male interactions in captive chimpanzees (de Waal 1982). Males changed their partner preferences between the more distant periods (i.e., the unstable and stable periods), supporting the importance of flexibility in affiliation patterns depending on the social context.

As expected based on previous studies (Nishida, 1983; Goodall, 1986; Mitani et al., 2000; Newton-Fisher, 2002), we found little evidence for durability in patterns of grooming between males, and only two of the five males had durable preferred male grooming partners. Male-male grooming patterns were correlated only between the unstable and recently stable periods, suggesting that after the male dominance hierarchy had stabilized grooming patterns shifted. These differences across periods could reflect flexible adjustments to patterns of support among males given that interactions between males are often opportunistic and related to shifting temporary alliances (Nishida, 1983; de Waal, 1989).

In line with previous reports (e.g. de Waal, 1984; Hemelrijk & Ek, 1991; Boesch & Boesch-Achermann, 2000; Watts, 2000; 2002) grooming reciprocity based on partner choice was detected but there was a striking contrast between females and males. Female-female grooming reciprocity was found within all three periods, consistent with Hemelrijk & Ek (1991). However, in all dyads involving males, grooming was reciprocated only during the stable period when the male hierarchy had been stable for two years. Previous studies have reported grooming reciprocity based on partner choice between males (e.g. Hemelrijk & Ek ,1991; Watts, 2002) including during periods without a clear alpha male. Whether our findings regarding male reciprocity reflect differences in social uncertainty, the lack of extensive kinship between males (Mitani, 2009), or the small number of males in the study group, requires further research, although it should be noted that we found the same pattern in female-male dyads.

The gradual alpha male replacement that occurred over two and a half years in our study is unusual. Data from the wild suggest that most replacements occur more rapidly lasting from one day (Kaburu et al., 2013) to several months (Riss & Goodall, 1977, Nishida, 1983, Newton-Fisher 2002, Muller 2002), although there may be variability within the same species depending on group composition (Teichroeb & Jack 2017). Alpha male replacements in captivity occur over a similar time frame to the wild, from two (Seres et al., 2001) to several months (de Waal, 1986). Thus, the longer replacement period in this study is not necessarily an artefact of captive conditions and may have been due to group dynamics. The formation of effective alliances with other adult males has been considered crucial in determining the outcome of the dominance challenge and the fate of defeated alpha males (Uehara et al., 1994; Hasegawa & Kutsukake, 2015). In our study, the incoming alpha male maintained durable preferred grooming partnerships with one male and two females, whereas the outgoing alpha male maintained such partnerships with four females. These differences may reflect the strategies adopted by each male (e.g. de Waal, 1989; Foster et al., 2009).

Our findings shed light on an understudied aspect of primate sociality, that is durability of affiliation patterns throughout social uncertainty, and contribute to our understanding of durability and flexibility of human and non-human social relationships. Social uncertainty in humans is associated with an increased probability of supporting a friend contrary to local rules, given the strong correlation between a composite index of economic, social and political instability and individuals' willingness to lie to help a friend (Hruschka, 2010). This finding highlights the importance of considering social uncertainty when investigating individuals' investment in social relationships. It is tempting to exclude periods of social uncertainty from analyses of the durability of interaction patterns (e.g. Gilby & Wrangham, 2008), but including them can draw attention to the relative patterns of flexibility and durability of social relationships and contribute to our understanding about their relative importance in the social arena. In this respect, our study contributes to the understanding of sex differences in chimpanzee behavior by examining the role social uncertainty in them. Overall, we found greater consistency in female-female than male-male grooming patterns, which is in agreement with previous research on sex differences. Our study also emphasizes the importance of maintaining long-term partners through periods of instability with more consistent grooming patterns for females and more flexible grooming patterns for males. Further research is needed to investigate the maintenance of durable relationships by means of social interactions other than grooming and across different types of social uncertainty. Our findings also illustrate that captive studies can provide ideal settings to examine the details for potential flexibility of social interactions in response to factors external to the interacting individuals, such as the gradual replacement of the alpha male.

ACKNOWLEDGEMENTS

We thank Chester Zoo for permission to conduct this study and Clare Caws for assistance with data collection. We also thank Nicholas Newton-Fisher and an anonymous reviewer for their helpful comments on the manuscript. We are grateful to the North of England Zoological Society for part-funding the data collection.

REFERENCES

Anderson, D.P., Nordheim E.V. & Boesch C. (2006). Environmental factors influencing the seasonality of estrus in chimpanzees. *Primates*, 47, 43-50.

Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20141261.

Arnold, K., & Whiten, A. (2003). Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: Tests of five explanatory models. *Behaviour*, 140, 519–552.

Baker, K.C., & Smuts,B.B. (1994). Social relationships of female chimpanzees: diversity between captive social groups. In: R. Wrangham, R. McGrew, F. de Waal, & P.G. Heltne (Eds.), Chimpanzee cultures (pp. 227-242). Harvard: Harvard University Press.

Beisner, B. A., Jin, J., Fushing, H., & Mccowan, B. (2015). Detection of social group instability among captive rhesus macaques using joint network modeling. *Current Zoology*, 61, 70-84.

Boesch, C., & Boesch-Achermann, H. (2000). The chimpanzees of the Taï forest: behavioural ecology and evolution. Oxford: Oxford University Press.

Bukowski, W.M., Newcomb, A.F., & Hartup, W.W. (1998). The company they keep: Friendships in childhood and adolescence. Cambridge: Cambridge University Press.

Capitanio, J. P., & Cole, S. W. (2015). Social instability and immunity in rhesus monkeys: the role of the sympathetic nervous system. *Phil. Trans. R. Soc. B*, 370, 20140104.

Caws C.E., Wehnelt, S., Aureli F. (2008). The effect of a new vertical structure in mitigating aggressive behaviour in a large group of chimpanzees (*Pan troglodytes*). *Animal Welfare*, 17, 149-154.

Clarke, F. M., & Faulkes, C. G. (1997). Dominance and queen succession in captive colonies of the eusocial naked mole–rat, *Heterocephalus glaber*. *Proceedings of the Royal Society of London B: Biological Sciences*, 264, 993-1000.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In: A. Whiten, & R.W. Byrne (Eds.), Machiavellian intelligence II: extensions and evaluations. Cambridge: Cambridge University Press.

de Vries, H. (1993). The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika*, 58, 53-59.

de Vries, H., Netto, W., & Hanegraaf, P. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, 125, 157–175.

de Waal, F.B.M. (1984). Sex differences in the formation of coalitions among chimpanzees. *Ethology & Sociobiology*, 5, 239-255.

de Waal, F.B.M. (1986). The brutal elimination of a rival among captive male chimpanzees. *Ethology & Sociobiology*, 7, 237-251.

de Waal, F.B.M. (1989). Chimpanzee politics. London: John Hopkins University Press.

de Waal, F. B., & Luttrell, L. M. (1988). Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, 9, 101-118.

Dunbar, R. I.M., (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121-131.

Dunbar, R. I., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*, 147, 775-803.

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C.M., Krupenye, C., Gilby, I.C., & Pusey, A.E. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Animal Behaviour*, 105, 139-152.

Foster, M.W., Gilby, I.C., Murray, C.M., Johnson, A., Wroblewski, E.E., & Pusey, A.E. (2009). Alpha male chimpanzee grooming patterns: implications for dominance “style”. *American Journal of Primatology*, 71, 136-144.

Fraser, O.N., Schino, G., & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, 114, 834–843.

Gilby, I.C., & Wrangham, R.W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology & Sociobiology*, 62, 1831-1842.

Goodall, J. (1986). The chimpanzees of Gombe. Cambridge, MA: Belknap Press.

Hemelrijk, C.K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour*, 39, 1013-1029

Hasegawa, M., & Kutsukake, N. (2015). Bayesian competitiveness estimation predicts dominance turnover among wild male chimpanzees. *Behavioral Ecology and Sociobiology*, 69, 89-99.

Hemelrijk, C.K., & Ek, A. (1991). Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour,* 41, 923-935.

Herzog, C. J., Czéh, B., Corbach, S., Wuttke, W., Schulte-Herbrüggen, O., Hellweg, R., ... & Fuchs, E. (2009). Chronic social instability stress in female rats: a potential animal model for female depression. *Neuroscience*, 159, 982-992.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.

Hruschka, D.J. (2010). Friendship: development, ecology, and evolution of a relationship. Berkley, CA: University of California Press.

Kaburu, S.S.K., Inoue, S., & Newton-Fisher, N. (2013). Death of the Alpha: Within-Community Lethal Violence Among Chimpanzees of the Mahale Mountains National Park. *American Journal of Primatology*, 75, 789–797.

Kahlenberg, S. M., Thompson, M. E., Muller, M. N., & Wrangham, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, 76, 1497-1509.

Kappeler, P. M., & Watts, D. P. (2012). Long-term field studies of primates. Berlin, Heidelberg: Springer-Verlag.

Koski, S.E., de Vries, H., van de Kraats, A., & Sterck, E.H.M. (2012). Stability and change of social relationship quality in captive chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 33, 905–921.

Koyama, N. F., Caws, C., & Aureli, F. (2012). Supply and demand predict male grooming of swollen females in captive chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 84, 1419-1425.

Krappmann, L. (1998). Amicita, drujba, shin-yu, philia, freundshaft, friendship: on the cultural diversity of a human relationship. In W.M. Bukowski, A.F. Newcomb, & W.W.

Kutsukake, N. (2009). Complexity, dynamics and diversity of sociality in group-living mammals. *Ecological Research*, 24, 521-531.

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71, 840-851.

Lehmann, J., & Boesch, C. (2008). Sex differences in sociality. *International Journal of Primatology*, 29, 65–81.

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77, 377–387.

Lehmann, J., Majolo, B., & McFarland, R. 2016. The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behavioral Ecology*, 27(1), 20-28.

Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2013). Male-female association patterns among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International Journal of Primatology*, 34, 917-938.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27, 209-220.

Manuck, S. B., Kaplan, J. R., & Clarkson, T. B. (1984). Social instability and coronary artery atherosclerosis in cynomolgus monkeys. *Neuroscience & Biobehavioral Reviews*, 7, 485-491.

Massen, J. J., Sterck, E. H., & De Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour*, 147, 1379-1412.

Massen, J.J.M., & Sterck, E.H.M. (2013). Stability and durability of intra-and intersex social bonds of captive rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 34, 770-791.

Matsumoto-Oda, A., Hosaka, K., Huffman, M.A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology*, 19, 999-1011.

Mitani, J.C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77, 633-640.

Mitani, J.C., Merriwether, D.A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, 59, 885-893.

Moscovice, L. R., Douglas, P. H., Martinez- Iñigo, L., Surbeck, M., Vigilant, L., & Hohmann, G. (2017). Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. *American Journal of Physical Anthropology*, 163, 158-172.

Muller, M. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), Behavioural diversity in chimpanzees and bonobos (pp.112-114). Cambridge: Cambridge University Press.

Muller, M., & Mitani, J. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, 35, 275–331.

Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: the infant safety hypothesis. *Behavioral Ecology and Sociobiology*, 59, 561-570.

Nakamichi, M., & Yamada, K. (2007). Long-term grooming partnerships between unrelated adult females in a free-ranging group of Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology*, 69, 652-663.

Newton-Fisher, N.E. (2002). Relationships of male chimpanzees in the Budongo Forest, Uganda. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), Behavioural diversity in chimpanzees and bonobos (pp. 125-137). Cambridge: Cambridge University Press.

Newton-Fisher, N. E. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology*, 27, 1589–1599.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale mountains. In D. A. Hamburg, & E. R. McGown (Eds.), *The Great Apes: Perspectives on Human Evolution* (pp. 73–121). Menlo Park, California: Benjamin & Cummings.

Nishida T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 24, 318–336.

Nishida, T. 1988. Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica*, 50, 109-123.

Noë, R.F., de Waal, F.B.M., & van Hooff, J.A.R.A.M. (1980). Types of dominance in a chimpanzee colony. *Folia Primatologica*, 34, 90-110.

Perry, S. (1998). A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). *Primates*, 39, 51-70.

Riss, D., & Goodall J. (1977). The recent rise to the alpha rank in a population of free-living chimpanzees. *Folia Primatologica*, 27, 134-151.

Royle, N. J., Pike, T. W., Heeb, P., Richner, H., & Kölliker, M. 2012. Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1749), 4914-4922.

Schino, G., & Aureli, F. (2017). Reciprocity in group-living animals: partner control *versus* partner choice. *Biological Reviews* 92, 665-672.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. 2010. Social bonds enhance reproductive success in male macaques. *Current Biology*, 20, 2207-2210.

Seres, M., Aureli, F., & de Waal, F. (2001). Successful formation of a large chimpanzee group out of two preexisting subgroups. *Zoo Biology*, 20, 501-515.

Silk, J.B. (2002). Using the'F'-word in primatology. *Behaviour*, 139, 421-446.

Silk, J. B., Alberts, S. C., & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, 302, 1231-1234.

Silk, J.B., Alberts, S.C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology & Sociobiology*, 61, 197-204.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... & Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 3099-3104.

Silk, J.B., Beehner, J.C., Berman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., … Cheney, D.L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology & Sociobiology*, 61, 197-204.

Silk, J.B., Alberts, S.C., Altmann, J., Cheney, D.L., & Seyfarth, R.M. (2012). Stability of partner choice among female baboons. *Animal Behaviour*, 83, 1511-1518.

Slater, K., Cameron, E., Turner, T., & du Toit, J.T. (2008). The influence of oestrous swellings on the grooming behaviour of chimpanzees of the Budongo Forest, Uganda. *Behaviour*, 145, 1235-1246.

Stanton, M. A., & Mann, J. 2012. Early social networks predict survival in wild bottlenose dolphins. *PloS One*, 7, e47508.

Stumpf, R. M., & Boesch, C. (2010). Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, 79, 333-342.

Teichroeb, J. A., & Jack, K. M. (2017). Alpha male replacements in nonhuman primates: Variability in processes, outcomes, and terminology. *American Journal of Primatology*, 79, e22674.

Uehara, S., Hiraiwa-Hasegawa, M., Hosaka, K., & Hamai, M. (1994). The fate of defeated alpha male chimpanzees in relation to their social networks. *Primates*, 35, 49-55.

Vigil, J.M. (2007). Asymmetries in the friendship preferences and social styles of men and women. *Human Nature*, 18, 143-161.

Wakefield, M.L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, 85, 1303-1313.

Watts, D. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, 21, 211-238.

Watts, D. (2002). Reciprocity and interchange in the social relationships of wild chimpanzees. *Behaviour*, 139, 343-370.

Wehnelt, S., Bird, S., & Lenihan, A. (2006). Chimpanzee forest exhibit at Chester Zoo. *International Zoo Yearbook*, 40, 313-322.

Weinstein, T.A., & Capitanio, J.P. (2012). Longitudinal stability of friendships in rhesus monkeys (*Macaca mulatta*): individual-and relationship-level effects. *Journal of Comparative Psychology*, 126, 97-108.

Wey, T. W., Burger, J. R., Ebensperger, L. A., & Hayes, L. D. 2013. Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour*, 85(6), 1407-1414.

Wrangham, R., Clarke, A., & Isabiryre-Basuta, G. (1992). Female social relationships and social organisation of Kibale Forest chimpanzees. In T. Nishida, W. McGrew, P. Marler, M. Pickford, & F.B.M. de Waal (Eds.), Topics in Primatology Volume 1, Human Origins (pp. 81-98). Tokyo: Tokyo University Press.

Table 1. Summary data showing distribution of grooming across the three periods

		Period		
		unstable	recently stable	stable
% of dyads in which grooming was observed	all dyads	60.3	66.2	69.1
	female-female dyads	43.9	60.6	69.7
	male-male dyads	80.0	90.0	70.0
	male-female dyads	75.0	88.3	66.7

Table 2. Correlations between periods for female-to-female grooming dyads.

Grooming given between years			Reciprocity in grooming		
Periods	$\tau_{rw;XY.Z}$	P	Periods	$\tau_{rw;XY.Z}$	P
unstable & recently stable	0.23	**0.006***	unstable	0.23	**0.004***
recently stable & stable	0.21	**0.008***	recently stable	0.28	**0.001***
unstable & stable	0.13	0.1	stable	0.67	**0.0002***

Partial Kendall rowwise correlations ($\tau_{rw;XY.Z}$) for female-to-female grooming dyads (with kinship held constant) between periods with varying stability in the male hierarchy (unstable, recently stable, and stable period) and reciprocity within each period. * Significant p values after sequential Bonferroni correction.

Table 3. Number of same-sex and different-sex durable preferred grooming partners for females and males.

subjects	Same-sex			Different-sex		
	no. durable preferred partners	no. related long-term preferred partners / no. close kin in group	mean (±SD) no. preferred grooming partners per period	no. durable preferred partners	no. related long-term preferred partners / no. close kin in group	mean (±SD) no. preferred grooming partners per period
F1	3	-	5.6 ± 1.5	0	-	4.0 ± 1.0
F2	0	-	2.3 ± 4.0	0	-/1	3.3 ± 0.6
F3	2	1/2	3.3 ± 1.5	1	-	4.7 ± 0.6
F4	2	1/2	3.7 ± 0.6	0	-	2.3 ± 0.6
F5	1	1/1	4.0 ± 1.0	0	-	1.3 ± 0.6
F6	2	1/1	4.7 ± 1.5	2	-	4.3 ± 0.6
F7	0	-/1	3.3 ± 0.6	2	-	4.7 ± 0.6
F8	2	-	5.3 ± 1.2	0	-	4.3 ± 1.2
F9	0	-	3.3 ± 0.6	2	-	4.3 ± 1.2
F10	1	0/1	5.3 ± 1.2	0	-	5.0 ± 0
F11	1	1/1	2.7 ± 1.5	1	-	4.0 ± 1.0
F12	1	1/1	2.3 ± 1.2	0	-	3.7 ± 0.6
M1-D	1	-	3.0 ± 0	3	0/1	5.7 ± 2.1
M2-B	0	-	2.7 ± 0.6	2	-	3.0 ± 1.0
M3-N	0	-/1	0.3 ± 0.6	1	-	4.3 ± 0.6
M4-F	1	0/1	3.3 ± 0.6	2	-	4.7 ± 0.6
M5-W	1	-	3.3 ± 0.6	0	-	3.7 ± 0.6

F=females; M=males; numbers following F and M serve to identify the 12 female and 5 male subjects.

Table 4. Correlations between periods for male-to-male grooming dyads.

Grooming given between years			Reciprocity in grooming		
Periods	τ_{rw}	P	Periods	τ_{rw}	P
unstable & recently stable	**0.47**	**0.003***	unstable	0.37	0.03
recently stable & stable	0.22	0.15	recently stable	0.28	0.12
unstable & stable	0.11	0.33	stable	**0.81**	**0.0007***

Kendall rowwise correlations (τ_{rw}) for male-to-male grooming dyads across periods with varying stability in the male hierarchy (unstable, recently stable, stable) and reciprocity within each period.

* Significant p values after sequential Bonferroni correction.

Table 5. Correlations between periods for male-to-female and female-to-male grooming dyads.

Grooming given between years			Reciprocity in grooming		
Periods	τ_{rw}	P	Periods	τ_{rw}	P
Male grooming females:					
unstable & recently stable	**0.31**	**0.007***	unstable	-0.05	0.4
recently stable & stable	**0.38**	**0.001***	recently stable	0.02	0.4
unstable & stable	-0.01	0.5	stable	**0.71**	**0.0005***
Female grooming males:					
unstable & recently stable	0.30	**0.011***	unstable	0.11	0.2
recently stable & stable	0.16	0.09	recently stable	-0.17	0.09
unstable & stable	0.14	0.1	stable	**0.56**	**0.0005***

Kendall rowwise correlations (τ_{rw}) for male-to-female and female-to-male grooming dyads across periods with varying stability in the male hierarchy (unstable, recently stable, stable) and reciprocity within each period.* Significant p values after sequential Bonferroni correction.