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Research article

Chimpanzee immigration: flexible social strategies lead to successful integration in a captive group

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Abstract

Chimpanzee (*Pan troglodytes*) inter-group encounters are typically aggressive in nature, as individuals have evolved the predisposition to jointly defend their home range against neighbouring groups. The current study presents data on the behavioural strategies of chimpanzees during the integration of one male and two females into a well-established group at Basel Zoo, Switzerland. Moreover, a full integration procedure is included. The study found that, as predicted, social relationships were generally of better quality in dyads of individuals from the same group than dyads of individuals from different groups shortly after integration. Interestingly, immigrants additionally targeted males as preferred interaction partners, contrary to observations in inter-group encounters. In addition, immigrants targeted the resident juveniles for play interactions, significantly more so than did residents. The alpha male policed the resident group members, further facilitating immigrant integration, including the integration of another male. In contrast, both resident and immigrant females had better relationships with members of their own group than with members of other groups. Overall, these diverse behavioural strategies led to the successful long-term integration of the immigrant individuals, a demonstration of the social flexibility of this species in contrast to the evolved xenophobic propensities seen in the wild.

Introduction

Chimpanzees (*Pan troglodytes*) usually act aggressively during inter-group contact or they may avoid each other altogether. They often patrol their territorial borders, sometimes engaging in lethal raids against neighbouring communities (Goodall 1986; Wrangham and Peterson 1996; Watts et al. 2002, 2006; Wilson et al. 2004, 2014; Sherrow and Amsler 2007; Schel et al. 2013). Although chimpanzees are highly xenophobic, they tolerate immigration from adolescent females, a strategy that limits inbreeding (Emery Thompson et al. 2006). Nulliparous immigrant females are generally well accepted by resident males, but resident females sometimes demonstrate aggressive behaviours against newcomers (Townsend et al. 2007; Kahlenberg et al. 2008). Little is known about male immigration, although it can happen under particular conditions (Sugiyama 1999). Unsurprisingly, the introduction of new chimpanzees in an established captive group could lead to strong aggressive reactions.

As part of an exchange to maintain genetic diversity as stipulated in the European Endangered Species Programme (EEP), Basel Zoo transferred two female chimpanzees and received two new females. Furthermore, because the Basel group included only one older male and two youngsters, Basel Zoo decided to introduce a new male who would eventually become the alpha male in the group. Normally, the EEP exchanges females but not males, to mimic natural events. This management system is fairly recent and Basel Zoo is "in transition" from the old management system. Similar procedures have previously been carried out before in other facilities (Seres et al. 2001; Schel et al. 2013), suggesting that chimpanzees can indeed deviate from their propensity

for hostility toward individuals from other groups. However, aggressive behaviours can occur in such cases, making safe integration a highly challenging task for keepers (Brent et al. 1997; Seres et al. 2001; Schel et al. 2013). Hence, more data about successful integration are needed; this study provides a full description of immigrant chimpanzee integration.

A couple studies have documented the integration of a group of chimpanzees into an established group (Seres et al. 2001; Schel et al. 2013). In one study, a 19-member group was formed from two sub-groups at the Yerkes Regional Primate Research Center (Seres et al. 2001). Intensity of aggression decreased between individuals over the following years, but grooming remained important in the chimpanzees' social lives. In another study, a group of 11 individuals from Beekse Bergen Zoo was integrated into a group at Edinburgh Zoo, which was also composed of 11 adult individuals (Schel et al. 2013). At the group level, the aggression rate quickly decreased between groups but remained stable between members of the same group. On the other hand, association and affiliative behaviours increased with time between groups.

While the decrease of aggression over time between captive chimpanzees from different groups is known, little is known about how individual chimpanzees achieved this decrease in aggressive behaviours.

The current study addressed this issue by analysing changes in relationships among dyads during the integration process. The aim was to better understand the different strategies used by individuals as a function of their sex, age, social role, and group membership. In line with reports from the wild, it was hypothesised that chimpanzees would prefer relationships with members of their own group and that adult males would associate with female, but not male, immigrants. We also predicted less prosocial behaviour between resident and immigrant females, as has been shown in studies in the wild (Kahlenberg et al. 2008).

Table 1. Description of reported behaviours.

Behaviour	Description
Grooming	According to Nishida et al. (1999) and described by Goodall (1989) as following: "...use both hands, pushing the hair back with the thumb or index finger of one hand and holding it back while picking at the exposed skin with the nail of the thumb or index finger of the other." Direction of grooming was specified, as well as partner identity.
Playing	According to Nishida et al. (1999), "Goodall (1989) divided play into lone play and social play. (…) She added that, "There is a facial expression connected with play, the play face, a type of locomotion that is seen only in the play context, the play walk, and a vocalization, laughing."
Pant-grunting	According to Nishida et al. (1999) and described by Goodall (1989) as "a series of soft or loud grunts functioning as a token of respect given during greeting by submissive chimpanzees and during submissive interactions..." Pant-grunt direction was specified.
Aggression	One individual or more attacked or threatened another one (Nishida et al. 1999). Actor and recipient identities were specified, as well as aggression severity (aggression severe: contact aggression including bite or hit; aggression chase: directed aggression with movement but without contact; aggression display: undirected aggression with movement or display; aggression threat: stationary display, bark).

Method

Data collection

The study was conducted between August 2013 and March 2014 with the chimpanzee group of Basel Zoo, Switzerland. The group initially consisted of one adult male (ER, 51 years), four adult females (JA, XD, BG, QM, ≥20 years), one adolescent female (ZA, 11 years), two juvenile males (CB and FA, 5 and 8 years) and one juvenile female (GS, 4 years). At the end of August 2013, two females (QM and ZA) were removed. One day after the removal, one male and two females arrived at Basel Zoo. Data were collected over a period of 7 months following introduction.

Measurements of behaviours, particularly using association between individuals and grooming rates, enable the determination of affinity in primates (Langergraber et al. 2009; Mitani 2009; Silk et al. 2003, 2006a, b). This is because, in a fission–fusion species such as chimpanzees, spatial associations between individuals highly depend on social group structures, while grooming is generally used in primates to form and strengthen social bonds.

For data collection on social interactions, one individual visible from the public viewing area was randomly selected and observed through focal sessions of one-hour each (Altmann 1974). If the focal individual was out of view more than 10 min during the first 15 min, a new focal session was started. Generally, six to nine focal sessions on different individuals were conducted per day. If one individual was followed for one hour on one day, it was not followed again during the same hour on other days until all other chimpanzees had been studied during this specific time period. Table 1 summarises the types of behaviours recorded in this study. Each instance of the listed behaviours observed during the focal session was recorded. Cases of resident policing (by vocalisations or by active physical intervention) during aggressive events involving immigrants versus residents were also recorded. Policing was defined as impartial interventions by third parties in conflicts but without aggression directed specifically at one contestant (Rudolf von Rohr et al. 2012). It is of note that ER largely policed by vocalisations and attempts to lead physical interventions, due to his physical condition. Conflicts including the immigrant females FI and GR were not analysed, as KU could have been perceived as either an immigrant protector or a resident by FI and GR (KU was integrated before FI and GR).

During each focal session, scan sampling was performed every 15 min to record the focal subject's location and the composition of its party. A party was defined as the association of individuals in the same sub-enclosure (there were six observable sub-enclosures, Figure 1). The identity and distance of the focal animal's nearest neighbour was also recorded. Data were collected at least five days per week during September and October and four days per month from November to March. Less data were collected during this second period because of the group's improved stability and because another project simultaneously being run by the data collector. FG collected all data from public viewing areas, between 0800 and 1800.

Data analysis

Observation times during which the focal individual was out of view were removed and only data from after the first immigrant individual was well integrated (9 September 2013) were used. This was two days after data on the first out-group dyad interactions were recorded and reduced the total observation time to 308.8 h.

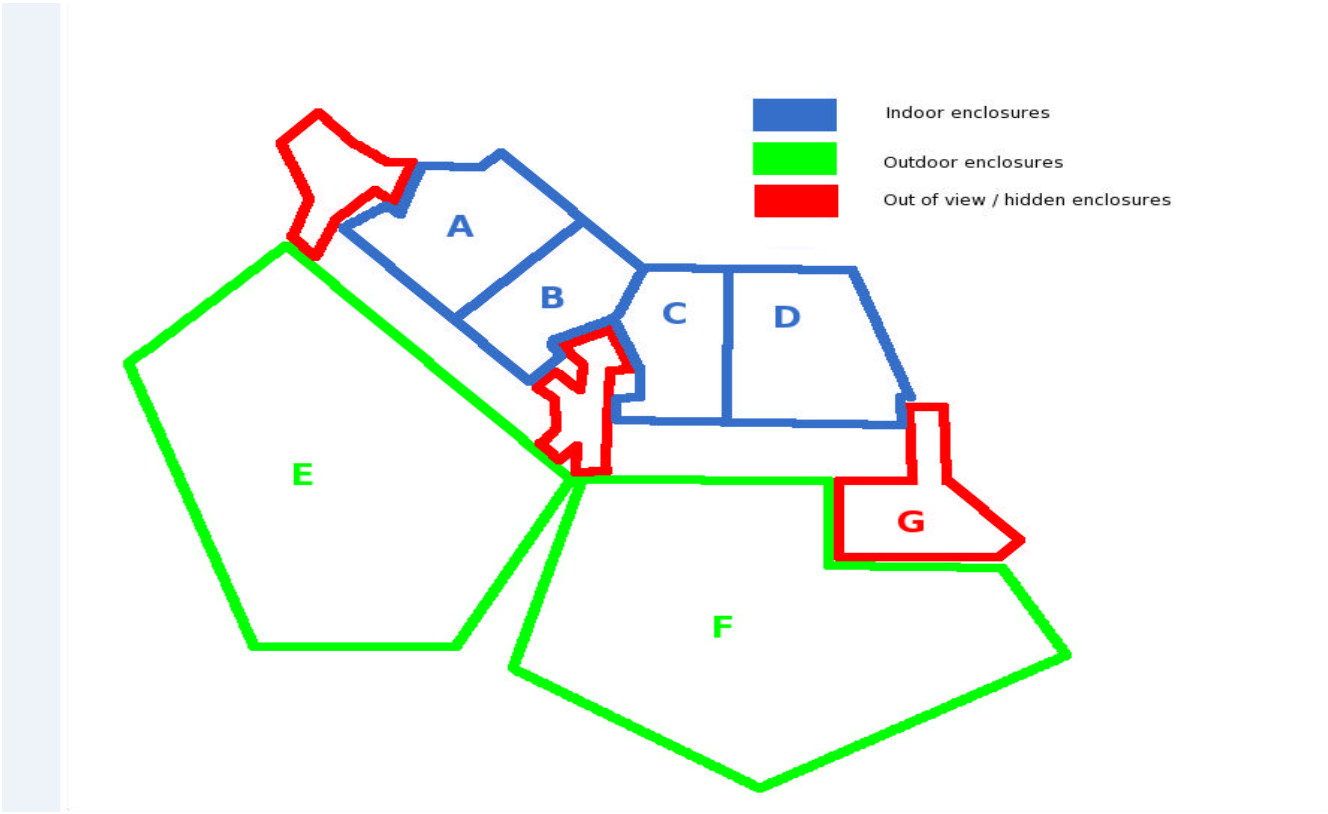

Figure 1. Floor plan of enclosures

Each of the 10 individuals was observed on average 30.9 h (range: 21.6 h–38.3 h; SD=4.9 h).

To monitor changes in social behaviour over time, the study period was divided into three sub-periods of approximately equal observation duration: early, middle and late integration. In addition, the primary stage of integration before these sub-periods, i.e. the initial time period after KU's integration but before FI and GR's arrival (FI and GR were excluded from data), were considered. The average visibility for all individuals was 8.2 h (range: 7.3 h–9.1 h; SD=0.9 h) for each sub-period.

To measure social interactions (which were then used as a proxy to describe inter-individual social relationships), a relationship index (RI) was calculated for each direction of a dyad (e.g. A-B and B-A). This was based on three distinct metrics: an association index, a nearest neighbour index and a grooming index, which are assumed to be reliable to this end in non-human primates (Silk et al. 2003, 2006a, b, 2013; Langergraber et al. 2009; Schel et al. 2013). Moreover, these interactions were measurable throughout the study and in the long term.

The association index was defined according to the formula (Wakefield 2013):

$$NAB / (NA + NB - NAB)$$

Where NAB is the number of scans in which A and B were associated with each other, i.e. were in the same party; NA is the number of scans in which A was observed; NB is the number of scans in which B was observed.

The nearest neighbour index was calculated for each dyad based on the distance between the focal and his or her nearest neighbour during each scan sampling. The nearest neighbour values (Xi) were calculated according to the following formula:

$$Xi = (Dmax + 1 – Di) / (Dmax + 1)$$

Where Dmax is the maximum distance ever recorded between a focal and its nearest neighbour and Di the estimated distance between the focal and its neighbour; which produced a range of values where 1 was attributed to individuals in contact with each other and smaller values to more distant nearest neighbours. Zero was attributed to individuals that have never been seen as nearest neighbours. The nearest neighbour index was defined as:

$$\Sigma XAB / \Sigma XA$$

Where ΣXAB is the sum of nearest neighbour values of distance in which B was A's nearest neighbour; and ΣXA the sum of values recorded for A.

The grooming index was determined in a similar way to Schel et al. (2013):

$$GAB / (TA + TB)$$

Where GAB is the total time in which A was observed grooming B; TA is the total time A was observed; TB is the total time B was observed. All three indices were standardised by dividing the respective mean value of each subject with a given index , such

Table 2. Information about chimpanzees composing the Basel group during study time.

Original group	Name	Code	Sex	Age	Rearing	Kinship	Note
Basel	Benga	BG	F	34	Nursery	GS Mother	
	Colebe	CB	M	8	Mother	Son of QM	
	Eros	ER	M	51	Wild	Father of BG, CB, FA, GS, XD	Suffers from partial paralysis due to arthritis. No longer sexually active
	Fahamu	FA	M	4	Mother		
	Garissa	GS	F	5	Mother		
	Jacky	JA	F	45	Wild	QM and ZA mother	
	Xindra	XD	F	38	Mother	FA mother	
Osnabrück	Kume	KU	M	10	Mother		
Leipzig	Fifi	FI	F	20	Mother	GR half-sibling	
	Gertude/Kitoko	GR	F	20	Mother	FI half-sibling	

that values less than 1 indicate a weak association (a low nearest neighbour or grooming rate) with a partner, and values greater than 1 indicate a stronger association (a high nearest neighbour or grooming rate) with a partner. The composite measure (RI) for each dyad was then defined as the mean of a dyad's three standardised scores akin to other frequently used sociality indices (Silk et al. 2003, 2013).

RI values indicated that an animal engaged in more positive behaviours with a partner when values were greater than 1 and fewer positive behaviours when values were less than 1.

The influence of the following six factors on the RI was investigated: i) relationship type: this specifies whether the subject and the partner came from the same group (in-group: Basel-Basel and Leipzig-Leipzig) or not (out-group: Basel-Leipzig, Basel-Osnabrück, Leipzig-Basel, Leipzig-Osnabrück, Osnabrück-Basel, Osnabrück-Leipzig); ii) subject sex (male, n=136; female, n=190); iii) partner sex (male, n=136; female, n=190); iv) subject age (juvenile, n=102; adult, n=224); v) partner age (juvenile, n=102; adult, n=224); vi) sub-period: defined as primary integration (9 September 2013 to 20 September 2013), early integration (26 September 2013 to 11 October 2013), middle integration (14 October 2013 to 4 December 2013) and late integration (14 January 2014 to 13 March 2014).

Social dominance ranks are known to have an impact on friendship in primates (Seyfarth and Cheney 2012), but the sample size for subject's pant-grunts (a reliable signal of sub-ordinance in chimpanzees; Laporte and Zuberbühler 2010) was too low to establish a clear female hierarchy, despite the knowledge of alpha male/female before integration (Baumeyer and Goetschi, personal observation). Moreover, the process of integration was likely to have an impact on dominance relations, introducing further confusion to hierarchies. For this reason, social rank was not included in the model.

Linear mixed model

Data were analysed with R v. 3.1.1 (R Core Team, 2014) with package "lme4" (Bates et al. 2014), "effects" (Fox and Hong 2009) and "car" (Fox and Weisberg 2011). To determine which factors had a significant influence on successful integration and the establishment of a chimpanzee's first relationships in a group, Linear Mixed Models (LMM) were constructed to explore the variation in association and sociality patterns (RI). The aforementioned exploratory factors were included as fixed factors and subject and partner identities were defined as random factors to control for pseudo-replication. As the effects of out-group relationships were of interest, the interaction between factors and the relationship type were also analysed. RI values were log-transformed to produce a normal distribution, with positive values indicating a stronger association and positive social behaviours and negative values indicating weaker associations and less positive social behaviours. Normal distribution of the model's residues and homogeneity of variance were checked visually. Likelihood ratio tests (LRT) were performed to remove non-significant interactions between fixed factors and to retain the model from which the main effects can be interpreted. Variance inflation factors (VIF) were checked with vif() function from "car" package (Fox and Weisberg 2011) derived from linear models with the random effects excluded. As all VIF were smaller than 1.2, it was assumed that co-linearity was not an issue in the models. The full model was compared to the null model with LRT to assess significance. The null model included only random factors.

Playing

During observations, it appeared that newly integrated chimpanzees spent considerable time playing with Basel juveniles. The study therefore analysed the percentage of time spent playing in order to see if newly integrated individuals spent significantly more time playing with juveniles than did resident Basel adults. However, as playing was not observed in each individual, these data are independently to RI. A LMM was used to explore playing time and the origin of the adult subject (immigrant or resident) was defined as a fixed factor and subject and partner identities as random factors to control for pseudo-replication. A LRT was used to assess model significance by comparison with the null model, which included only random factors.

Table 3. Results of the LMM testing differences in RI.

	Estimate	SE	t-value	P-value
Intercept	-1.14	0.31	(a)	
Relationship type				
In-group	1.73	0.35	(a)	
Partner sex				
Male	0.41	0.22	(a)	
Subject sex				
Male	0.37	0.16	(a)	
Period				
Early	0.84	0.30	(a)	
Middle	0.75	0.30	(a)	
Late	0.84	0.30	(a)	
Partner age				
Juvenile	0.03	0.20	0.13	0.897
Subject age				
Juvenile	-0.05	0.13	-0.40	0.689
Relationship type : partner sex				
In-group : male	-1.04	0.24	-4.37	<0.001
Relationship type : subject sex				
In-group : male	-0.67	0.21	-3.13	0.002
Relationship type : period				
In-group : early	-1.04	0.36	-2.93	0.004
In-group : middle	-0.86	0.36	-2.41	0.017
In-group : late	-0.93	0.36	-2.61	0.010

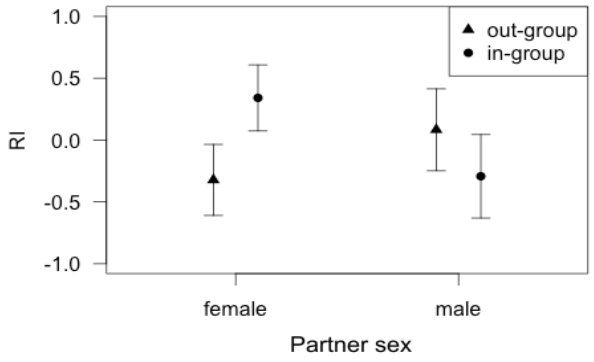

Figure 2. Distribution of RI according to relationship type and partner sex. Shown are estimated marginal means and 95% confident intervals according to model predictions.

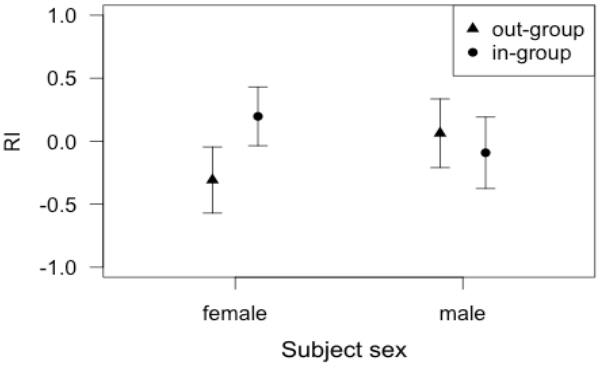

Figure 3. Distribution of RI according to relationship type and subject sex. Shown are estimated marginal means and 95% confident intervals according to model predictions.

Results

Integration procedure

On 4 September 2013, two Basel females (QM and ZA) were separated from the Basel group and were sent to zoos in Leipzig and Osnabrück, respectively. On 5 September, one male (KU; Table 2), and two females (FI and GR) arrived at Basel Zoo and were kept isolated from physical contact with the local chimpanzees. FI and GR, both from Leipzig, were kept together in the same sub-enclosures (F and G, Figure 1), while KU, originating from Osnabrück, was housed alone in sub-enclosure D. Sub-enclosures C and E were kept empty.

KU was introduced first to the Basel group. On 7 September the highest-ranking resident female, JA, was allowed physical contact with KU in sub-enclosure C, and less than one hour later the resident adult male, ER, joined them. One hour later KU was introduced to the entire Basel group, at which point sub-enclosure D was accessible for Basel chimpanzees. Basel chimpanzees initiated some aggression (including chases and hits) but without any major injury (not requiring veterinary intervention). CB was the first resident to initiate physical contact by briefly grooming KU after he calmed down.

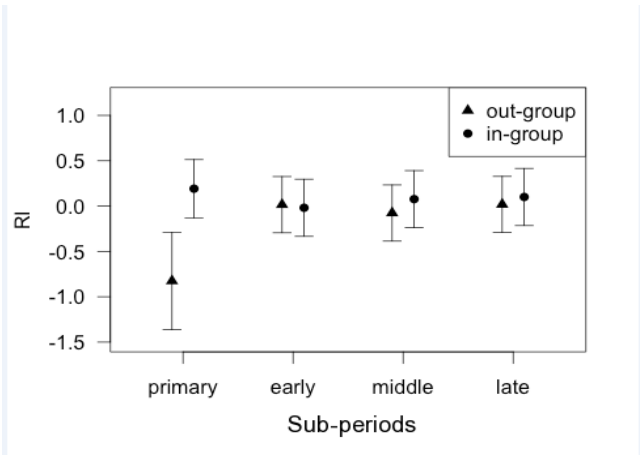

Figure 4. Distribution of RI according to relationship type and sub-periods. Shown are estimated marginal means and 95% confident intervals according to model predictions.

Table 4. Results of the LMM testing differences in Playing.

	Estimate	SE	t-value	P-value
Intercept	1.49	0.27	(a)	
Adult origin				
Resident	-1.39	0.31	-4.43	<0.001

The Leipzig chimpanzees were introduced on 21 September to the alpha male (ER) and to the newly introduced male (KU) in sub-enclosures C and D (sub-enclosure B was kept empty during this time) for one hour before being separated again. Males displayed frequently but both Leipzig chimpanzees showed submissive behaviours (e.g. presenting genitals and pant-grunting) and spent a few minutes grooming males. Grooming was sometimes reciprocal and males also groomed females. Over the following days, they were similarly introduced to JA (with ER and KU), then to XD and her son FA (still with ER and KU) the next day, and sub-enclosure B was open to allow contact through barred doors with the rest of the group. Two hours later, the doors were opened to bring the entire group together. Aggression occurred particularly between immigrant and resident females, including chases, hits, hits with sticks through barred doors and bites, but again no major injury was reported. Aggression generally took place at the beginning of the contact phases. During the whole integration procedure, the keepers let immigrant chimpanzees inspect empty sub-enclosures as often as possible according to daily cleaning routines and by avoiding indirect contact with other chimpanzees (a sub-enclosure always separated them). From 26 September onwards, all chimpanzees were in a single group.

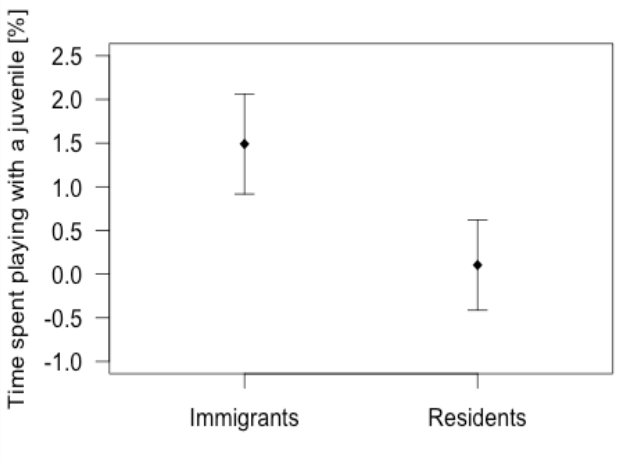

Figure 5. Distribution of percentage of observed time spent playing with CB, FA or GS according to adult origin. Shown are estimated marginal means and 95% confident intervals according to model predictions.

Relationship index

The model significantly differed from its null model (χ^2=33.98, df=13, P=0.001; Table 3). There were significant time and sex effects in the RI Linear Mixed Model when these factors were in interaction with relationship type (Table 3). The interaction between relationship type and partner sex revealed a significant difference in RI distribution (estimate=-1.04, SE=0.24, P<0.001; Table 3), in that individuals showed higher RI values when interacting with females from their own group than with out-group female partners. Conversely, individuals had higher RI values with out-group males than with in-group male partners (Figure 2). Similarly, there was an interaction of relationship type and sex in the RI distribution for subjects (estimate=-0.67, SE=0.21, P=0.002; Table 3). Males had higher RI values with out-group members than with members from their own group, while females had higher RI values when observed in in-group dyads than in out-group dyads (Figure 3).

Interestingly, age had no effect on RI values (partner age: estimate=0.03, SE=0.20, P=0.897; subject age: estimate=-0.05, SE=0.13, P=0.689; Table 3).

Concerning time period, the RI values fluctuated with time, particularly during the early period of integration. A significant interaction was also found between relationship type and sub-period (early: estimate=-1.04, SE=0.36, P=0.004; middle: estimate=-0.86, SE=0.36, P=0.017; late: estimate=-0.93, SE=0.36, P=0.010; Table 3). RI values were lower at the beginning of the study between out-group members, but increased during early period and then remained stable (Figure 4). Moreover, initial contacts were largely aggressive between out-group members (Baumeyer and Goetschi, personal observation). In in-group dyads, the RI decreased after primary integration but then remained stable and at high levels (Figure 4).

Aggression

The Basel adult male ER was observed policing during conflict (at least by vocalising) in 16 of the 25 aggressive interactions in which the immigrant male KU was victimised by Basel chimpanzees during primary and early introduction periods.

Playing

The model explores playing time according to the origin of the adult subject (immigrant or resident). By assessing the model versus the null model, it was found that adult origin had a significant effect on the time spent playing with a juvenile (χ^2=10.95, df=1, P=0.001; Table 4). The immigrant females FI and GR and the immigrant male KU played significantly more with each juvenile than the resident females XD, BG, JA and the resident male ER (Figure 5).

Discussion

Chimpanzees are naturally inclined to react xenophobically to out-group members of their own species (Wilson et al. 2014) and, as predicted, individuals initially had few positive social interactions with immigrants when one male and two females were introduced. However, similarly to previous studies (Brent et al. 1997; Seres et al. 2001; Schel et al. 2013), the results show that chimpanzees are very capable of effectively coping with the artificial situation of immigration.

Relationship index

In this study, RI values were used as an indication of chimpanzees' preference for particular partners. However, one possible weakness of this index is that it is mainly based on association rate and proximity, meaning it could be interpreted as a measure of an individual's monitoring of another chimpanzee or bi-products of concentrated foods and not a measure of positive social

interactions. However, association is considered a tactical decision and chimpanzees demonstrated a preference for association partners (Newton-Fisher 1999). One direction for future work would be to include more socio-positive behaviours in this index (e.g. gentle touches, embraces and kisses). It is difficult to determine whether certain behaviour could impact more than others upon relationships, and composite standardised indices could be less biologically meaningful than thought (Silk et al. 2013). However, as the goal was to compare the results with other studies, RI was used as a reliable reflection of physical association and grooming preference, which are a proxy for socialisation (Langergraber et al. 2009) and used as a standard measure for positive social behaviour in primates (Silk et al. 2006a, b).

The fact that individuals initially showed more positive social behaviours in in-group dyads is in line with group-level integration in another captive group (Schel et al. 2013).

Sex and positive behaviour

The results show various deviations from the general pattern of xenophobia. First, males, and particularly ER, the old resident alpha male, did not behave xenophobically by associating more with out-group members than in-group members. For males, socio-positive behaviour towards immigrant females is unsurprising, mainly because immigrant females provide additional mating opportunities. This behaviour could also be explained by ER's social role as the alpha male in which he acted as mediator by protecting newly integrated chimpanzees during conflict. Male policing behaviour during social conflict has been repeatedly observed in the wild (Townsend et al. 2007; Kahlenberg et al. 2008), suggesting that males associate preferentially with immigrants to protect them. High-ranking males appear to be motivated to secure social stability within a group, something that has been observed in captive groups after the arrival of new immigrants (Rudolf von Rohr et al. 2012). However, counter to expectations, was that ER's behaviour was not limited to the female immigrants, but was also exhibited when interacting with the immigrant male. It is possible that ER's advanced age, health problems and unusual standing as a single male was responsible for his friendly behaviour towards the male immigrant.

As mentioned, contrary to males, females preferred in-group dyads over out-group dyads. This female behaviour is in line with field observations, which have been explained in terms of competition for resources (Muller 2007; Kahlenberg et al. 2008). However, such a competition only plays a minor role in captive individuals. This is in line with the propensity to react xenophobically, despite favourable ecological constraints.

Finally, when comparing RI according to partner sex, it was found that out-group males were preferred over in-group males. This could be explained by immigrant females looking for protection from the resident alpha male (ER) and by interacting much with the resident juvenile males . At the same time, the resident females appeared to favour the immigrant male KU, who might have been more sexually attractive than the resident male.

Age and friendship

Overall, age had no effect on RI values. This means that adults and juveniles did not differ in their grooming and association behaviours. However, immigrants spent significantly more time playing with juveniles than did residents, including their mothers. KU was still an adolescent (11 years at the end of the study), so this may have been a bi-product of a normal development (Palagi 2007), although it does not explain the increased play behaviour by the adult immigrant females (FI and GR). Playing has been interpreted as a means to prevent conflict and to promote tolerance during feeding, and to allow individuals to assess social bonds (Palagi et al. 2004; Palagi 2007). More generally, juveniles are easier to approach, less aggressive and more curious than are adults. As such, juveniles facilitated contact between members of different groups by building a social bridge between immigrants and adult residents. Seres et al. (2001) noticed the same phenomenon during the formation of a large chimpanzee group out of two pre-existing subgroups.

Although RI did not differ according to age, it probably plays a role in introduction success. Immigrant chimpanzees were young and the resident alpha male very old. This implies a reduced physical strength and less aggressive behaviours.

The development of friendships

Relationships between in-group and out-group members changed with time. RI values between out-group members quickly improved, while relationships between in-group members decreased somewhat after the primary integration period. This peak during primary integration could reflect the tendency of resident chimpanzees to first strengthen their existing bonds in reaction to immigrant arrival (and resident departure) before addressing immigrants as seen in a previous study (Schel et al. 2013). In this study, the effect may have been largely driven by the immigrant male KU, who was integrated during primary introduction. In general, however, integration proceeded considerably faster in this study than in the Schel et al. (2013) study, probably due to the smaller number of immigrants (Basel n=3; Edinburgh n=11), which is likely to favour contact between residents and immigrants. Similarly, in humans, enforced social contact is known to decrease prejudice and aggressive tendencies toward out-group members (Struch and Schwartz 1989; Sigelman and Welch 1993; Turner et al. 2008).

Implications for captive care

The present study indicated that the focal group of captive chimpanzees is more socially flexible than reported in wild groups. While the Basel chimpanzees enjoyed both easier ecological conditions and slightly altered conditions compared to those in the wild, the results suggest that successful integration of new chimpanzees into a pre-existing group is possible, even for genetically unrelated males. This is indicative both of a species-wide capacity for behavioural flexibility depending on the situation, as well as the fact that captive groups of chimpanzees may be successfully enlarged in non-standard ways (e.g. with the transfer of males).

In this case, it appeared that males (particularly the alpha male) played the most important role in the integration process and facilitated out-group relations more than did females. Moreover, by playing, juveniles probably facilitated the introduction of immigrant individuals. While this is at odds with the current view of males being the more violent sex (Wilson et al. 2014), it is important to remember that, for males, the integration of new females carries direct fitness benefits. In addition, in this study, the resident male had no other mature male by his side, as would normally be the case in the wild, which may have changed his behaviour in significant ways. In this study, females established fewer relationships with out-group members and mostly preferred to associate with members of their own group, except the out-group males. Even so, relations between out-group members improved with time. Overall, this study is another demonstration of the high social flexibility of this species, which enables individuals to achieve group-level outcomes that differ per situation. The results are likely to have been influenced by enforced social contact, which pressured individuals into establishing good relationships between residents and immigrants. Without enforced contact, individuals could leave and not interact with each other, complicating the establishment of relationships in a limited time.

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References

Altmann J. (1974) Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Bates D., Mächler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. doi:10.18637/jss.v067.i01.

Brent L., Kessel A.L., Barrera H., (1997) Evaluation of introduction procedures in captive chimpanzees. *Zoo Biology* 16: 335–342.

Emery Thompson M., Newton-Fisher N.E., Reynolds V. (2006) Probable Community Transfer of Parous Adult Female Chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology* 27: 1601–1617.

Fox J., Hong J. (2009) Effect displays in R for multinomial and proportional-odds logit models: Extensions to the effects package. *Journal of Statistical Software* 32: 1–24.

Fox J., Weisberg S. (2011) *An R companion to applied regression*, 2nd edn. Sage, Thousand Oaks.

Goodall J. (1989) *Glossary of Chimpanzee Behaviors*. Jane Goodall Institute, Tucson.

Goodall J. (1986) *The Chimpanzees of Gombe: Patterns of Behavior*. Belknap Press of Harvard Univ. Press, Cambridge.

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.

Kitchen D.M., Cheney D.L., Seyfarth R.M. (2004) Factors Mediating Inter-Group Encounters in Savannah Baboons (*Papio cynocephalus ursinus*). *Behaviour* 141: 197–218.

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

Laporte M.N., Zuberbühler K. (2010) Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour* 80: 467–473.

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

Muller M.N. (2007) Chimpanzee violence: Femmes fatales. *Current Biology* 17: R365–R366.

Newton-Fisher N.E. (1999) Association by male chimpanzees: a social tactic? *Behaviour* 136: 705–730.

Nishida T., Kano T., Goodall J., McGrew W., Nakamura M. (1999) Ethogram and ethnography of Mahale chimpanzees. *Journal of Anthropological Science* 107: 141–188.

Palagi E. (2007) Play at work: revisiting data focusing on chimpanzees (*Pan troglodytes*). *Journal of Anthropological Science* 85: 153–164.

Palagi E., Cordoni G., Borgognini-Tarli S.M. (2004) Immediate and delayed benefits of play behaviour: new evidence from chimpanzees (*Pan troglodytes*). *Ethology* 110: 949–962.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Rudolf von Rohr C., Koski S.E., Burkart J.M., Caws C., Fraser O.N., Ziltener A., van Schaik C.P. (2012) Impartial Third-Party Interventions in Captive Chimpanzees: A Reflection of Community Concern. *PLoS ONE* 7: e32494.

Schel A., Rawlings B., Claidiere N., Wilke C., Wathan J., Richardson J., Slocombe K. (2013) Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology* 75: 254–266.

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

Seyfarth R.M., Cheney D.L. (2012) The Evolutionary Origins of Friendship. *Annual Review of Psychology* 63: 153–177.

Sherrow H.M., Amsler S.J. (2007) New Intercommunity Infanticides by the Chimpanzees of Ngogo, Kibale National Park, Uganda. *International Journal of Primatology* 28: 9–22.

Sigelman L., Welch S. (1993) The Contact Hypothesis Revisited: Black-White Interaction and Positive Racial Attitudes. *Social Forces* 71: 781.

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. (2006a) Social relationships among adult female baboons. Variation in the quality and stability of social bonds. *Behavioural Ecology & Sociobiology* 61: 197–204.

Silk J.B., Altmann J., Alberts S.C. (2006b) Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioural Ecology & Sociobiology* 61: 183–195.

Silk J., Cheney D., Seyfarth R. (2013) A practical guide to the study of social relationships: A Practical Guide to the Study of Social Relationships. *Evolutionary Anthropology Issues News and Reviews* 22: 213–225.

Struch N., Schwartz S.H. (1989) Intergroup aggression: its predictors and distinctness from intra-group bias. *Journal of Personality & Social Psychology* 56: 364.

Sugiyama Y. (1999) Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates* 40: 61–68.

Townsend S.W., Slocombe K.E., Thompson M.E., Zuberbühler K. (2007) Female-led infanticide in wild chimpanzees. *Current Biology* 17: R355–R356.

Turner R.N., Hewstone M., Voci A., Vonofakou C. (2008) A test of the extended intergroup contact hypothesis: The mediating role of intergroup anxiety, perceived ingroup and outgroup norms, and inclusion of the outgroup in the self. *Journal of Personality & Social Psychology* 95: 843–860.

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.P., Muller M., Amsler S.J., Mbabazi G., Mitani J.C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology* 68: 161–180.

Watts D.P., Sherrow H.M., Mitani J.C. (2002) New cases of inter-community infanticide by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* 43: 263–270.

Wilson M.L., Boesch C., Fruth B., Furuichi T., Gilby I.C., Hashimoto C., Hobaiter C.L., Hofmann G., Itoh N., Koops K., Lloyd J.N., Matsuzawa T., Mitani J.C., Mjungu D.C., Morgan D., Muller M.N., Mundry R., Nakamura M., Pruetz J., Pusey A.E., Riedel J., Sanz C., Schel A.M., Simmons N., Waller M., Watts D.P., White F., Wittig R., Zuberbühler K., Wrangham R.W. (2014) Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* 513: 414–417.

Wilson M.L., Wallauer W.R., Pusey A.E. (2004) New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology* 25: 523–549.

Wrangham R.W., Peterson D. (1996) *Demonic Males: Apes and the Origins of Human Violence*. Houghton Mifflin, New York.