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RESEARCH ARTICLE

Network Analysis of Social Changes in a Captive Chimpanzee Community Following the Successful Integration of Two Adult Groups

ANNE MARIJKE SCHEL[1], BRUCE RAWLINGS[1], NICOLAS CLAIDIÈRE[2], CLAUDIA WILKE[1], JEN WATHAN[1], JO RICHARDSON[3], SOPHIE PEARSON[3], ELIZABETH S. HERRELKO[3,4], ANDREW WHITEN[2], AND KATIE SLOCOMBE[1]*
[1]*Department of Psychology, University of York, York, United Kingdom*
[2]*Centre for Social Learning and Cognitive Evolution, School of Psychology, University of St Andrews, St Andrews, United Kingdom*
[3]*Royal Zoological Society of Scotland, Edinburgh Zoo, Edinburgh, United Kingdom*
[4]*Department of Psychology, University of Stirling, Stirling, United Kingdom*

Chimpanzees are highly territorial and have the potential to be extremely aggressive toward unfamiliar individuals. In the wild, transfer between groups is almost exclusively completed by nulliparous females, yet in captivity there is often a need to introduce and integrate a range of individuals, including adult males. We describe the process of successfully integrating two groups of chimpanzees, each containing 11 individuals, in the Budongo Trail facility at the Royal Zoological Society of Scotland's Edinburgh Zoo. We use social network analysis to document changes in group dynamics within this population over the 16 months following integration. Aggression rates were low overall and members of the two original groups engaged in significantly fewer aggressive interactions over time. Association and grooming data indicate that relationships between members of the original groups became stronger and more affiliative with time. Despite these positive indicators the association data revealed the continued existence of two distinct subgroups, a year after integration. Our data show that when given complex space and freedom to exhibit natural fission–fusion groupings, in which the chimpanzees choose whom they wish to associate and interact with, the building of strong affiliative relationships with unfamiliar individuals is a very gradual process. Am. J. Primatol. 00:1–13, 2012.

Key words: social network analysis; chimpanzee; integration; social relationships

INTRODUCTION

Many social animals actively defend a territory, which provides the group with access to valuable resources including food, water, and mates [e.g., Emlen & Oring, 1977; Mosser & Packer, 2009; Wrangham, 1981]. Defense of a territory can involve the use of vocal or olfactory signals to announce ownership of the territory to nongroup members as well as physical aggression toward intruders or neighboring groups during encounters at boundaries [Cant et al., 2002; Kitchen & Beehner, 2007; McComb et al., 1994]. Chimpanzees have repeatedly been found to engage in intense and occasionally lethal aggression toward individuals from neighboring communities [Goodall et al., 1979; Watts et al., 2002, 2006; Wilson et al., 2004]. Within a community chimpanzees are characterized by fission–fusion dynamics (individuals form fluid subgroups whose composition changes, as individuals choose to leave and join these groups). Male chimpanzees, who stay in their natal groups, usually form close relationships with other males and participate in cooperative boundary patrols, which sometimes become raiding parties into neighboring territories [Goodall, 1986; Mitani & Watts, 2005]. Attacks on males from rival communities can be particularly violent [e.g., Goodall et al., 1979; Watts et al., 2006]. For example, in Gombe, Tanzania, one community killed all adult males in a neighboring community, leading to the dissolution of that community [Goodall, 1986]. A similar case was suspected in Mahale, Tanzania [Nishida et al., 1985].

In the wild the only habitually nonviolent intergroup contact involves the transfer of young, nulliparous estrus females between groups [Boesch &

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*Correspondence to: Katie Slocombe, Department of Psychology, University of York, York YO10 5DD, United Kingdom. E-mail: katie.slocombe@york.ac.uk

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Boesch-Achermann, 2000; Goodall, 1986]. Resident males usually readily accept these females into their community, making communities more genetically diverse. There have been a few observations at different sites of parous females and their offspring immigrating or visiting communities and receiving minimal or no aggression from the resident community members [Boesch et al., 2008; Emory-Thompson et al., 2006; Nishida & Hiraiwa-Hasegawa, 1985]. However, these events are rare and counterbalanced by reports of killing of the offspring of extracommunity parous females [e.g., Watts et al., 2002].

Despite the prevalence of hostility between strangers in the wild, in captivity it is often necessary to introduce new chimpanzees to existing groups or to integrate individuals from different groups for a variety of management reasons, such as veterinary care, breeding programs, formation of geriatric groups, spacing constraints, rehoming of problematic individuals or the dissolution of animal collections. Such introductions and integrations may not mirror natural intergroup interactions and thus may produce several sources of stress to the individuals involved. Introductions often involve transportation to a new location and adaptation to a new enclosure both of which can induce physiological and behavioral changes.

A recent study that examined the response of chimpanzees to transportation and relocation revealed that this process resulted in weight loss and a variety of physiological changes, some of which persisted for 3 months posttransportation [Schapiro et al., 2012]. Hormonal and behavioral analysis of black tufted-ear marmosets who had formed a pair shortly before relocation to a new enclosure, indicated that cortisol levels remained elevated for 8 weeks after the relocation event. In contrast, the relocation of a well-established pair resulted in no elevation in cortisol levels, but a significant increase in time spent in close proximity. These instances indicate that strong social relationships can reduce the potential stress involved in physical relocation [Schaffner & Smith, 2005]. Further evidence of social regrouping as a strategy to combat stress induced in moving to a new enclosure comes from a recent study on the immediate effects of relocation in squirrel and capuchin monkeys to the Living Links to Human Evolution Research Centre in Edinburgh Zoo [Dufour et al., 2011]. Individuals maintained closer proximities with each other after relocation and in both species there was evidence of changes in the social structure of the groups after relocation (e.g., change in identity of individuals at the centre of the social network).

The relocation of captive primates to novel physical environments can lead to significant hormonal, behavioral, and social changes, but when a novel social environment is simultaneously introduced, this creates an even bigger challenge of maintaining primate well-being. In highly territorial species such as chimpanzees, introductions to new social groups are particularly difficult to manage. Successful introductions of infants who have been hand-raised following maternal rejection or young individuals (1- to 8-year-old) who arrive at sanctuaries have been reported [Bashaw et al., 2010; Mukoda & Tweheyo 2007]. In these cases, initial integration with dominant females seems to have aided their successful integration with the rest of the group. Introduction of adults is more problematic. Alford et al. [1995] found that 8% of adult–adult introductions resulted in wounds being suffered by one or both parties. Wounds were more likely to occur in male–male introductions, with 50% of the wounds inflicted requiring surgical intervention. The rearing history of the individuals also seemed to influence the outcome, with integrations of individuals with different rearing histories (e.g., mother or human raised) being less successful [Alford et al., 1995]. Brent et al. [1997] reported a similar pattern of introductions involving adult males being less successful than those involving females.

In this article, we present a systematic analysis of the social changes in a newly integrated chimpanzee community over the 16 months following integration of two established adult groups at the Budongo Trail facility at the Royal Zoological Society of Scotland's Edinburgh Zoo (further abbreviated as Edinburgh Zoo). We employ social network analysis (SNA) methods [Whitehead, 2008, 2009] to monitor the changing dynamics of the whole community over time. This technique has been successfully applied to a variety of primate species and research questions, offering a powerful tool for examining how behavior, at both an individual and group level, changes through time (see Sueur et al., 2011a for a review). To our knowledge this is the first study to examine how primate social networks change following integration with another group. In chimpanzees, examination of grooming networks in captivity has revealed that often a few central individuals are important to maintaining group cohesion [Kanngiesser et al., 2011]. When given an enclosure large and complex enough to allow natural fission–fusion behavior, SNA revealed that the affiliation and association networks of captive chimpanzees housed in the Budongo Trail facility, Edinburgh Zoo, were highly correlated and that aggression levels were low [Clark, 2011]. The subjects of Clark's study constitute the original resident group in the present study, allowing us to examine changes in relationships as a result of introduction of the second group. For example, we examined whether Cindy, who was identified by Clark [2011] as a peripheral member of the original community, changed her role following the introduction of 11 new individuals.

On the basis of the primate literature reviewed above, we predicted that given the Budongo Trail facility has sufficient space to allow the formation of subgroups, individuals would initially prefer to associate and affiliate within their original groups, with high aggression levels between groups. We predicted that with time, associations and active affiliative behavior between members of the original two groups would increase and aggression decrease. We predicted that the introduction of unfamiliar individuals would initially facilitate the strengthening of close bonds between the original Edinburgh group members, but that this would weaken over time. We predicted a similar pattern for the relocated Beekse Bergen group, but to a more exaggerated extent, as they were dealing with a new physical as well as social environment, so overall there would be a greater need for social support from established associates.

METHODS

Participants and Study Site

Research was carried out at the Budongo Trail facility at Edinburgh Zoo. The Budongo Trail is a large exhibit with three interconnected 12 × 12 × 14 m indoor enclosures and an extensive outdoor area covering 1,832 m^2. The indoor sections, called "pods," have varying temperatures, lighting levels, and flooring materials. Both the indoor and outdoor areas have a range of beams, poles, ropes, nets, and ledges for climbing and nesting and are connected by a series of tunnels. The chimpanzees are fed up to eight times a day at irregular intervals with a wide variety of foods. During the day, chimpanzees are free to go wherever they choose, except when individual areas are being cleaned. This makes the complex Budongo Trail facility highly unusual for a captive facility as it allows the chimpanzees to adopt their natural fission–fusion social system, where they can use these different spatial areas to choose who to associate with and who to avoid.

Observations took place between 8:00 a.m. and 17:00 p.m. from the public viewing areas, or in the off-show bed area. We started data collection on a total of 22 chimpanzees (N = 11 males and N = 11 females, aged between 11 and 49 years; see Table I for details), originating from two separate subgroups: Edinburgh Zoo and Beekse Bergen. Unfortunately, one adult male, Bram, died of natural causes 7 months after data collection had begun, so his data were subsequently removed from data analysis, leaving $N = 21$. Table I provides a summary of demographic information, as well as intragroup matrilineal information.

Procedure for Integration

The two groups of chimpanzees were initially kept physically and visually separated, although they had auditory and olfactory contact. In the first week after arrival (March 18, 2010) the Beekse Bergen group was gradually introduced to each area of the facility, so they became familiar with their new physical surroundings before meeting the other group. The two groups were then allowed visual contact in the off-show bed area under keeper supervision in the following week. Each group could access one side of the bed area, which consisted of five interconnected cages, with the middle cage securely locked to ensure no physical contact between groups was possible. During these sessions of visual contact, the keepers monitored behavioral reactions of individuals (see Table II) and individuals displaying affiliative or neutral behavior were identified as individuals suitable for early integration.

TABLE I. Demographic and Rearing Information of the Subjects

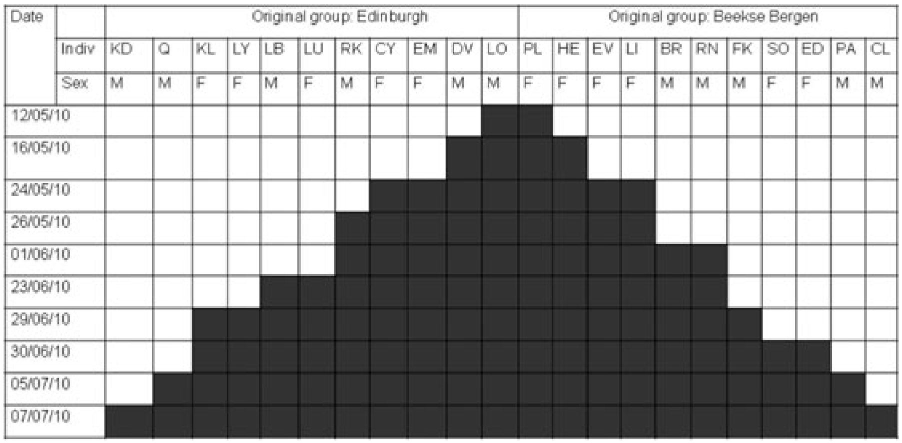
Group	Name	Code	Sex	Age	Mother	Rearing history
Beekse Bergen	Claus	CL	M	16	EV	Nursery
	Frek	FK	M	16		Mother
	Paul	PA	M	16		Mother
	Rene	RN	M	16		Nursery
	Edith	ED	F	13	EV	Mother
	Eva	EV	F	29		Nursery
	Heleen	HE	F	18		Mother
	Lianne	LI	F	20		Mother
	Pearl	PL	F	40		Wild
	Sophie	SO	F	28		Nursery
Edinburgh	David	DA	M	34		Mother
	Kindia	KD	M	12	LY	Mother
	Liberius	LB	M	10	LU	Mother
	Louis	LO	M	34		Wild
	Qafzeh	Q	M	17	EM	Mother
	Ricky	RK	M	48		Wild
	Cindy	CD	F	46		Wild
	Emma	EM	F	28		Mother
	Kilimi	KL	F	16	LY	Mother
	Lucy	LU	F	33		Mother
	Lyndsey	LY	F	25	CD	Mother

Note: Ages are for January 2010.

TABLE II. Key Behaviors [van Hooff, 1971; Goodall, 1986] Monitored during Visual or Physical Integration Sessions

Behavior	Definition
Affiliative	Play, grooming, grunting, and lip smacking
Neutral	Relaxed state in presence of others, minimal interaction
Aggressive	Intimidation displays, threat gestures, contact aggression
Fearful	Bared teeth facial expression, prolonged submissive crouching, hiding, and active avoidance of others

The process of physical integration was achieved through the creation of a third mixed group, into which individuals from the original two groups were gradually introduced. This ensured that individuals had social support from existing familiar group



Date		Original group: Edinburgh											Original group: Beekse Bergen										
	Indiv	KD	Q	KL	LY	LB	LU	RK	CY	EM	DV	LO	PL	HE	EV	LI	BR	RN	FK	SO	ED	PA	CL
	Sex	M	M	F	F	M	F	M	F	F	M	M	F	F	F	F	M	M	M	F	F	M	M
12/05/10												■	■										
16/05/10											■	■	■	■									
24/05/10									■	■	■	■	■	■	■	■							
26/05/10								■	■	■	■	■	■	■	■	■							
01/06/10								■	■	■	■	■	■	■	■	■	■	■					
23/06/10						■	■	■	■	■	■	■	■	■	■	■	■	■					
29/06/10				■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■				
30/06/10				■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		
05/07/10			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
07/07/10		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

Fig. 1. Illustration of the process of integration of individuals into the third mixed group. A shaded cell indicates that individuals left their original group and became part of the mixed group. The dominant males from each group (Claus, CL; Paul, PA; Kindia, KD; Qafzeh, Q) were the last to be introduced.

members while meeting new individuals and it allowed keepers to keep a relatively neutral balance of dominance between members of the two original groups. Figure 1 shows the order and timescale over which different individuals were successfully introduced to the third group. The founding members of the third group were chosen on the basis of their affiliative and neutral reactions to visual encounters with the other group. Individuals identified as vulnerable (e.g., RK: physically weak, LB: subordinate) by the keepers were integrated in the middle of the process to ensure they were well established in the third group with social support available before the most dominant individuals were introduced, at the end.

Introduction of new individuals into the third group started with visual contact in the bed area, followed by the opening of one door to allow limited physical contact between individuals through the mesh. Once affiliative or neutral behaviors were observed through the mesh, full physical access was given. The chimpanzees were then kept together in the bed area for as long as possible, where keepers had the opportunity to intervene if necessary. Intimidation displays and mild contact aggression (brief hits or slaps) were relatively common at this stage and keepers were only on stand-by to separate individuals if severe contact aggression occurred (biting, prolonged beating). If consistent aggressive or fearful behavior was observed, the new individuals were separated from physical contact and left in visual contact overnight and then the process of physical integration began again in the morning. However, if neutral and affiliative behaviors were observed, the group with the new members was then released from the bed area into one of the indoor enclosures. The pace of introductions was firmly dictated by the chimpanzees' behavior and reactions and the success of this integration was in part due to the capacity of this facility to comfortably hold three groups, meaning the integration process was not rushed. The keepers' knowledge of these individuals and accurate reading of their behavior was also of central importance in this process. No chimpanzee sustained an injury requiring surgical intervention during this process of integration.

Behavioral Observations Postintegration

Data were collected by AS, BR, CW, JW, SP, and six other keepers and research assistants over a 16-month period (July 2010 to October 2011) following the successful integration of the 22 chimpanzees into a single community. Training for all data collectors was provided by AS and KS and collected data were checked on at least a weekly basis to ensure correct entry into datasheets and that data collection protocols were adhered to. All researchers were tested by the keepers on their accuracy of identifying individuals and behaviors before they started data collection.

This study adhered to the American Society of Primatologists principles for the ethical treatment of primates and was approved by the ethics committee of the Department of Psychology, University of York. Association and interaction data were collected on 301 days over this period, with an uneven distribution of data collection over different months.

Association data

Association data were recorded using two methods: instantaneous scan sampling of group composition and focal sampling of nearest neighbors [Altmann, 1974]. Due to the spatial layout of the enclosure, the composition of subgroups in particular spatial locations was indicative of chimpanzees' association preferences [Clark, 2011]. Data were collected from five locations (i.e., three indoor pods, outside and the bed area) and individuals were considered to be part of the same subgroup if they were in the same indoor area or within 30 m of each other outside. A 10-min interval scans of subgroup composition were recorded for up to 1 hr in a single observation period. Due to the temporal dependence of multiple scans taken within a single observation period, only the first scan of each observation period was used in the analysis, giving a total of 321 scans for analysis. Observation periods were separated by at least 1 hr and were balanced between mornings and afternoons and between the different locations. Within an observation period, 10-min focal samples were conducted between scan samples. At the start of each focal observation a point sample of the identity and distance of the focal individual's nearest neighbor was recorded. Focal individuals were either chosen randomly from the available chimpanzees being observed, or we chose the individual for whom we had least focal samples recorded. Each individual was focal sampled only once within an observation period. We collected a total of 1,141 focal samples, which were distributed relatively evenly over the 21 individuals (mean number of samples/individual = 54.33, SD = 5.88, range = 40–63). In order to control for the variation in total focal samples from each individual, nearest neighbor data were analyzed as proportions (e.g., proportion of A's focal samples where B was nearest neighbor to A).

Interaction data

We recorded all grooming bouts that occurred within each observation period (in the location being observed). These all-occurrence data [Altmann, 1974] served as an index of affiliative interactions between individuals. The duration of all dyadic grooming bouts was recorded along with the identity of the individuals involved and whether simultaneous grooming between partners (mutual grooming) had occurred within the grooming bout. We recorded a total of 727 grooming bouts over 190.85 hr of observation.

We also recorded all aggressive interactions that occurred within each observation period (in the location being observed). For each aggressive interaction we recorded the identity of the aggressor and the victim, as well as the type of aggression. We distinguished between directed aggression where there was a clear victim (contact aggression, chasing or threatening with arm raise or ground slap) and intimidation displays where there was no clear target (charging, displacing objects without deviating to chase a specific individual). For analysis, we considered only directed aggression and thus focused on the 185 aggression bouts where at least one individual victim could be identified. These 185 bouts were recorded over 166.35 hr of observation.

All-occurrence grooming and aggression data could not be collected during all observation periods, because new researchers began by collecting only focal and scan data, before adding grooming, and finally the more challenging aggression data, to their observations. Hence the total period of all-occurrence data collection for these behaviors is different and smaller than the total observation period for the association data.

Simple correlational analyses were performed to track changes in grooming and aggressive interactions over time, with particular attention given to interactions between individuals from different original groups. The grooming data were also central to the SNA.

Social Network Analysis

SNAs use association and interaction data to create a synthetic representation of the social relationships of individuals within a group, the so-called social structure of a group [Hinde, 1976; Whitehead, 2008]. The use of SNA for the study of animal behavior is growing rapidly [Croft et al., 2008, 2011; Krause et al., 2009; Sih et al., 2009; Sueur et al., 2011a; Wey et al., 2008; Whitehead, 2008, 2009] because it allows the precise description and quantification of animal social relationships and therefore their comparison between groups and species [Sueur et al., 2011b] or across time [Dufour et al., 2011; Henzi et al. 2009]. We used SNA to describe and quantify the dynamics of the social relationships between the newly integrated chimpanzees across time. More precisely, we were interested in the effects of the potential disruption represented by the integration of the two groups of chimpanzees and the reorganization that followed. To do this, we constructed matrices of association and grooming data and analyzed the results using SOCPROG 2.4 [Whitehead, 2009].

Association data

We used two independent measures of association: (1) a proximity index computing the proportion of focal samples where each pair of individuals was recorded as nearest neighbors (e.g. number of focal samples of A where B is nearest neighbor + number of focal samples of B where A is nearest neighbor/total number of focal samples for A + total number of focal samples for B); and (2) an association index computing the proportion of scans in which a pair of individuals were observed in the same group (i.e., present within 30 m of each other outside or in the same inside enclosure area) of individuals (number of scans A + B both present/number of scans A present + number of scans B present). We constructed association matrices from the two indexes using SOCPROG 2.4 [Whitehead, 2008, 2009].

The two association matrices obtained from these two different indexes were highly correlated (Dietz R-test [Dietz, 1983] with 10,000 permutations, $R = 0.87, P < 0.001$). We therefore constructed a composite association index, combining the nearest neighbor and group-scan data. Thus, each association coefficient represented the proportion of scans the pair of individuals had been observed either as nearest neighbors or as part of the same group of individuals.

Interaction data

In the case of grooming, we first calculated the mean proportion of time one individual spent grooming another one (duration A grooms B/total duration A and B were observed together). We then divided the proportion of time spent grooming for each dyad by the mean proportion of time dyads spent grooming across the group. This gave a distribution of scores for which one was the average proportion of time a pair spent grooming and for which higher values represented dyads with stronger bonds than expected, and lower values for those that had weaker bonds [King et al., 2008, 2009; Sueur et al., 2011b]. Unfortunately, the total number of aggressive interactions for each dyad during the study period was too small to produce a clear network of dominance hierarchy (most dyads were involved in only one or no fights over the whole study period).

Network Statistics and Sociograms

Sociograms were designed using NetDraw [Borgatti, 2002]. Sociograms provide visual representations of associations or interactions between a set of individuals. Nodes (individuals) are linked by lines representing associations or interactions, the thickness of which corresponds to the strength of the relationship between the dyad.

We analyzed eigenvector centrality (henceforth “centrality”) in order to establish the connectedness between one individual and other individuals in the network [Newman, 2004]. The centrality index of an individual increases with the number and strength of its connections and when these connections are established with other central individuals (individuals who themselves have numerous and strong connections).

Modularity and Cluster Analysis

Clusters of individuals within communities are identified as having stronger relationships amongst themselves compared with other members of the group. SOCPROG 2.4 allows analysis of modularity so that association indices are stronger within subgroups and weaker between subgroups [Whitehead, 2008, 2009]. Modularity is calculated as the difference between the proportion of total associations within subgroups and the expected proportion given the total associations of each individual. Higher scores indicate closely bonded subgroups within communities and lower scores suggest a homogeneous social network within the community. A modularity value greater than 0.3 is usually considered to indicate useful divisions of the data [Newman, 2004]. We used the modularity technique to assess the social contacts between and within the Edinburgh and Beekse Bergen groups.

We also performed a hierarchal cluster analysis using the average linking method of SOCPROG 2.4 [Whitehead, 2008, 2009]. This technique generates a dendrogram in which the individuals are represented on one axis, and their associations on the other axis [Whitehead, 2008, 2009]. A cophenetic clustering coefficient was then calculated to assess whether the dendogram reliably represents the associations between individuals. A cophenetic clustering coefficient above 0.8 is usually considered sufficient for this [Sokal & Rohlf, 1962]. Hierarchal cluster analysis is appropriate for establishing marked subgroups within communities.

Time Periods

In order to examine how the relationships between the Beekse Bergen and Edinburgh chimpanzees developed over time postintegration, we focused on two phases; an early phase from July to December 2010 (135 days of observation over 6 months) and a later phase from April to October 2011 (117 days of observation over 7 months).

Statistical Analyses

Due to the relatively small sample sizes, nonparametric tests were used to compare behavior between groups (Mann–Whitney U test) and across time periods (Wilcoxon signed-rank test). Pearson’s correlations were conducted to establish associations between weeks elapsed since integration and both mutual grooming and aggression rates. All these statistical tests were performed in SPSS 19.

RESULTS

Intergroup and Intragroup Agonistic and Affiliative Interactions

Directed aggressive interactions

Of the 185 directed aggression bouts observed, the Edinburgh group performed 55.73% of these acts, whereas the Beekse Bergen group contributed with 44.27% of aggressive acts. Individual contribution to this total number of aggressive interactions differed (Table III), usually with the older and more established individuals of the original groups (Table I) performing more aggressive acts than younger members. Furthermore, males tended to be more aggressive than females, with the occurrence of male–male aggression being most prevalent (male–male aggression = 38.88% of overall aggressive interactions, male–female = 33.84% of overall

TABLE III. Individual Variation in Directed Aggressive Acts ($N = 185$) Performed by Members of the Original Edinburgh and Beekse Bergen Groups

Group	ID	Percentage of original group's total aggressive acts	Percentage of overall total aggressive acts
Beekse Bergen	Claus	32.94	14.58
	Frek	2.35	1.04
	Paul	24.71	10.94
	Rene	9.41	4.17
	Eva	12.94	5.73
	Edith	11.76	5.21
	Heleen	1.18	0.52
	Lianne	4.71	2.08
	Pearl	0.00	0.00
	Sophie	0.00	0.00
Edinburgh	David	9.35	5.21
	Kindia	5.61	3.13
	Liberius	23.36	13.02
	Louis	23.36	13.02
	Qafzeh	24.30	13.54
	Ricky	0.00	0.00
	Cindy	0.93	0.52
	Emma	7.48	4.17
	Kilimi	3.74	2.08
	Lucy	1.87	1.04
	Lyndsey	0.00	0.00

Note: The percentage each individual contributed to both their original group's total number of directed aggressive acts and the total number of directed aggressive acts observed are provided.

aggressive interactions, female–male aggression = 17.68% of overall aggressive interactions and female–female aggression = 9.60% of overall aggressive interactions).

Data were recorded on a total of 42 separate weeks in the postintegration study period and overall directed aggression rates were low (1.09 directed aggression events per hour). To be able to conduct more detailed analysis, all weeks with a total observation period of less than 1 hr were removed, leaving a total of 34 weeks of aggression data available for analysis. Within these 34 weeks the mean observation time was 4.76 hr/week (SD = 5.24) and the mean aggression rate was 1.24 bouts (SD = 1.43) of directed aggression per hour.

Overall, the aggression rates were slightly higher between groups (mean = 0.65 bouts per hour, SD = 1.15) than within groups (mean = 0.47 bouts per hour, SD = 0.92). In order to chart how aggression changed with time it was necessary to remove some data points that were outliers (more than 3 SD from the mean) in their respective data sets, meaning the analysis and figures are based on 32 (between groups) and 33 (within groups) weeks of data, respectively. Pearson's correlations revealed that intergroup (Edinburgh vs. Beekse Bergen) aggressive interactions significantly decreased over time ($r = -0.359$, $P = 0.044$, two-tailed; Fig. 2A), while intragroup aggressive interactions remained stable over time ($r = 0.037$, $P = 0.837$, two-tailed; Fig. 2B). It is important to note that the same pattern of results holds if outliers are included in the data set.

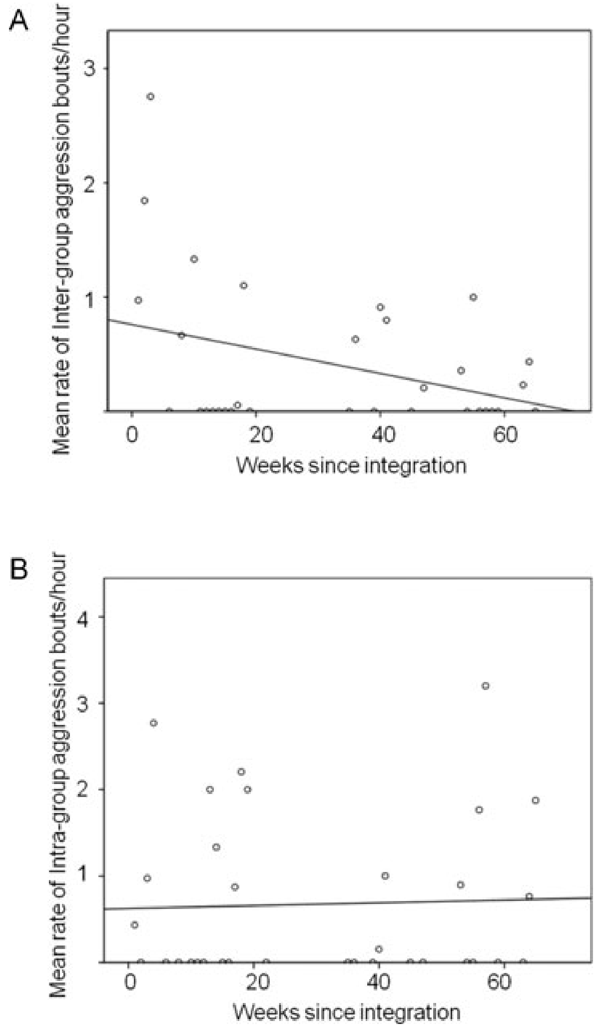


Fig. 2. Scatterplots illustrating the mean rate of aggression bouts per hour that occurred during (A) intergroup interactions (Edinburgh vs. Beekse Bergen) and (B) intragroup interactions. Lines of best fit are illustrated.

Grooming interactions

Data were recorded on a total of 45 separate weeks in the study period. All weeks with a total observation period of less than 1 hr were removed from data analysis, leaving a total of 38 weeks of grooming data for analysis. Within these 38 weeks the mean observation time was 4.77 hr/week (SD = 5.22). Finally, a few weeks that were identified as clear outliers (grooming rate more than 3 SD from the mean) were excluded, meaning the analysis and figures are based on 36 (between groups) and 37 (within groups) weeks of data, respectively.

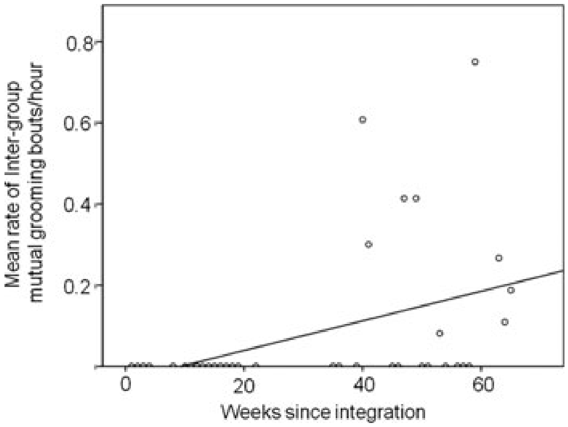


Fig. 3. Scatterplot showing the mean rate of intergroup mutual grooming bouts per hour over the study period. Line of best fit is illustrated.

Overall, grooming patterns were explored as part of the Social Network Analyses section below. Here we considered mutual grooming within a bout, as this type of grooming has been identified as a good indicator of strong social bonds between grooming partners [Fedurek & Dunbar, 2009]. We found there was a significant increase in intergroup mutual grooming bouts over time (Pearson's $r = 0.414$, $P = 0.012$, two-tailed, Fig. 3), but that rates of intragroup mutual grooming bouts remained stable over time ($r = 0.056$, $P = 0.741$, two-tailed).

Social Network Analyses

Association patterns

As predicted, the study of both the modularity and dendrograms revealed a split between the two groups that persisted for the entire study period, although it weakened with time. As can be seen in Figure 4, the maximum modularity for both the early and late period was high (equal to or above 30%) and the best division occurred neatly between the Edinburgh and the Beekse Bergen groups (as shown by the dendrograms). The maximum modularity however, decreased between the early (40%) and the late (30%) period. This is linked to the fact that the average composite association index between groups was smaller in the early period (mean = 0.035, 95% CI = [0.031; 0.039]) than in the later period (mean = 0.044, 95% CI = [0.040; 0.048]; Wilcoxon signed-rank test $Z = -4.25$, $P < 0.001$) and this increase was at the expense of within-group associations (early association mean = 0.221, 95% CI = [0.214; 0.228]; late association mean = 0.148, 95% CI = [0.141; 0.154]; Wilcoxon signed-rank test $Z = -11.72$, $P < 0.001$). The presence of two distinct subgroups and increasing associations between members of the two original groups over time was also apparent in the sociograms (Fig. 5). During the early period, all strong intergroup bonds centered on Edith, a young adult female originating from the Beekse Bergen group (Fig. 5A). Her role became less central in the later period, when more individuals interacted across the two original groups (Fig. 5B). The strength of the division between the two groups therefore decreased between the early and the late period, both because within groups associations decreased and between groups associations increased.

Furthermore, based on previous studies [e.g., Dufour et al., 2011; Schaffner & Smith 2005] we also predicted that the integration would create a strengthening of existing close bonds within the original groups and that this effect would be stronger for the relocated Beekse Bergen chimpanzees than the resident Edinburgh ones. As predicted, we found that the median centrality index of the Beekse Bergen chimpanzees was larger than that of the Edinburgh ones (Fig. 5), both in the early period (Beekse Bergen group median = 0.25, Edinburgh group median = 0.18; Mann–Whitney $U = 0.00$, $z = -3.91$, $P < 0.001$) and the later period (Beekse Bergen group median = 0.25, Edinburgh group median = 0.17; Mann–Whitney $U = 0.00$, $z = -3.89$, $P < 0.001$). Finally, Table IV gives an overview of the centralities of all group members and their change over time (i.e., between the early and late study periods).

Grooming patterns

The grooming data largely confirmed the association patterns described above. The grooming coefficient between groups increased over time (Wilcoxon signed-rank test $Z = -2.95$, $P < 0.001$), from 0.16 on average during the early period (95% CI [0.06; 0.27]) to 0.44 during the late period (95% CI [0.24; 0.64]). In contrast, there was no significant difference in grooming within groups between the two periods ($Z = -0.11$, $P = 0.91$). The within-group grooming coefficient was 1.92 on average during the early period (95% CI [1.41; 2.43]) and 1.51 on average during the late period (95% CI [1.19; 1.83]). This suggests that at first individuals might have concentrated on their long-term partners, with grooming therefore mainly occurring within the original groups. Later, when the two groups started to associate more, they appeared to have broadened their circle of grooming partners to include members of the other group.

DISCUSSION

The successful integration of two groups of adult chimpanzees into a single community of 21 individuals without serious injury is a remarkable feat, considering the highly territorial, xenophobic and aggressive nature of the species and the documented difficulties with previous integrations [Alford et al., 1995; Brent et al., 1997]. We suggest that the success of this integration is due to the use of the slow and

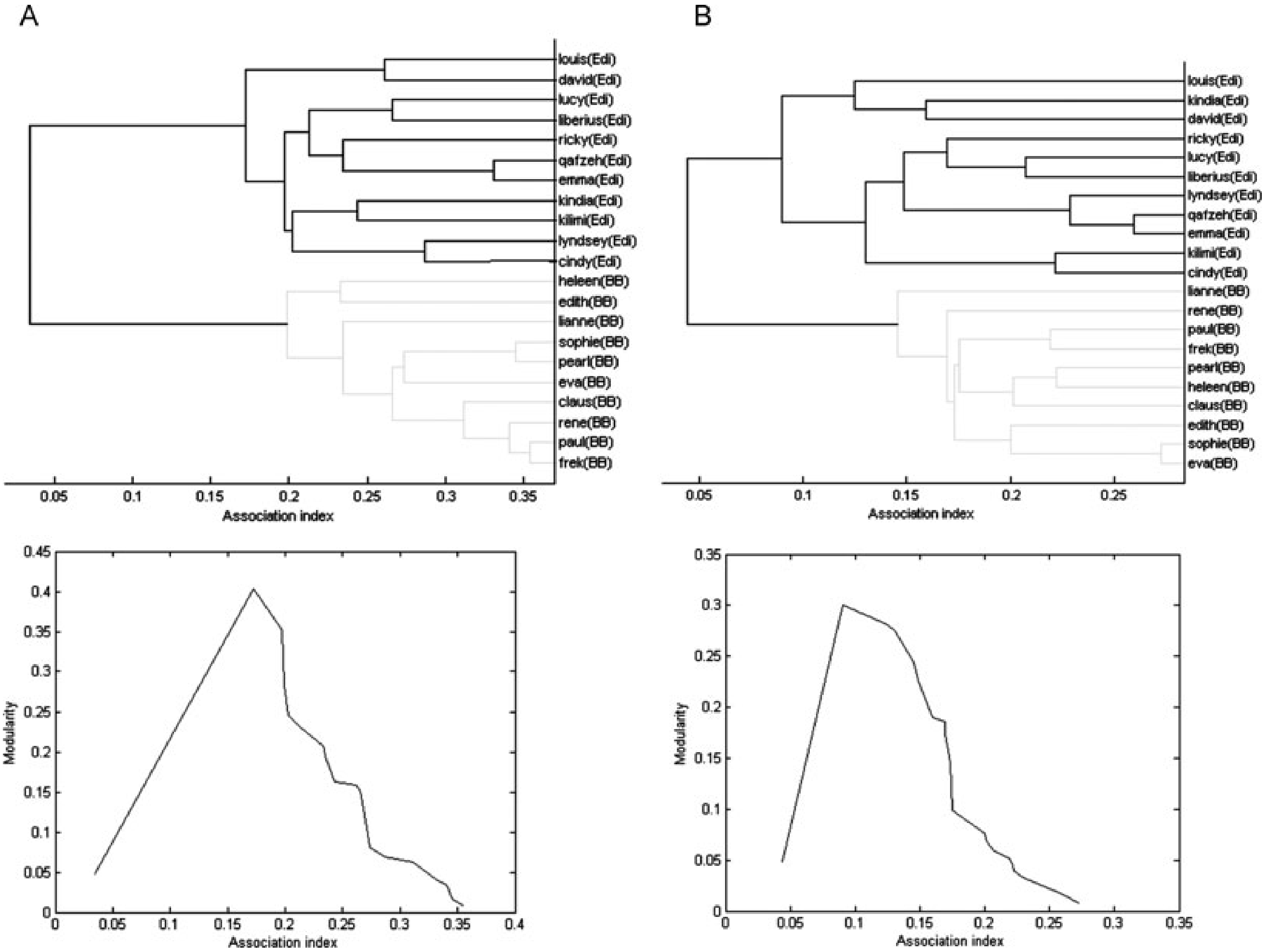


Fig. 4. Dendrogram and modularity for (A) the early period (Cophenetic correlation coefficient of 96% and maximum modularity of 40%) and (B) the late period (Cophenetic correlation coefficient of 92% and maximum modularity of 30%). Dendrograms produced using the "Average" method and cluster analysis using "Gregariousness" setting in SOCPROG. Cophenetic correlation coefficients above 80% are usually considered reliable [Sokal & Rohlf, 1962] and modularities greater than about 0.3 are usually considered to indicate useful divisions of the data [Newman, 2004].

gradual introduction methods we outlined in this article combined with the complex physical environment that enabled and supported this process. As we only studied the integration process of two groups within this unusual enclosure, the extent to which these methods would be successful in different locations is, however, unknown. We would encourage others to publish the immediate and long-term success of different introduction methods, to allow for more direct comparison of the efficacy of different methods. Unusually, in this study, we have not only been able to document the immediate integration process, but also to provide long-term data on the changing dynamics of the integrated community.

These long-term data indicate that aggression levels remained low and agonistic interactions between the original groups decreased significantly with time. This is particularly interesting when the territorial and aggressive nature of well-bonded communities of wild chimpanzees is considered [Goodall, 1986; Mitani & Watts, 2005]. The evenly matched number of adult males in the two original groups may have made serious physical aggression a highly risky and dangerous strategy that both groups have avoided. Previous work in the wild has shown that chimpanzees are adept at assessing the direction and magnitude of any numerical advantage in intergroup encounters and are more likely to avoid contact with neighbors if they do not have such an advantage [Wilson et al., 2001]. The spatial complexity of the enclosure enabled effective retreat from aggressive encounters and the avoidance of less familiar individuals and it is likely that this was key to the relatively low levels of aggression observed.

Conversely, grooming interactions that bridge the old group divide have increased with time. In line with Clark's [2011] findings, the association and grooming networks we identified were closely

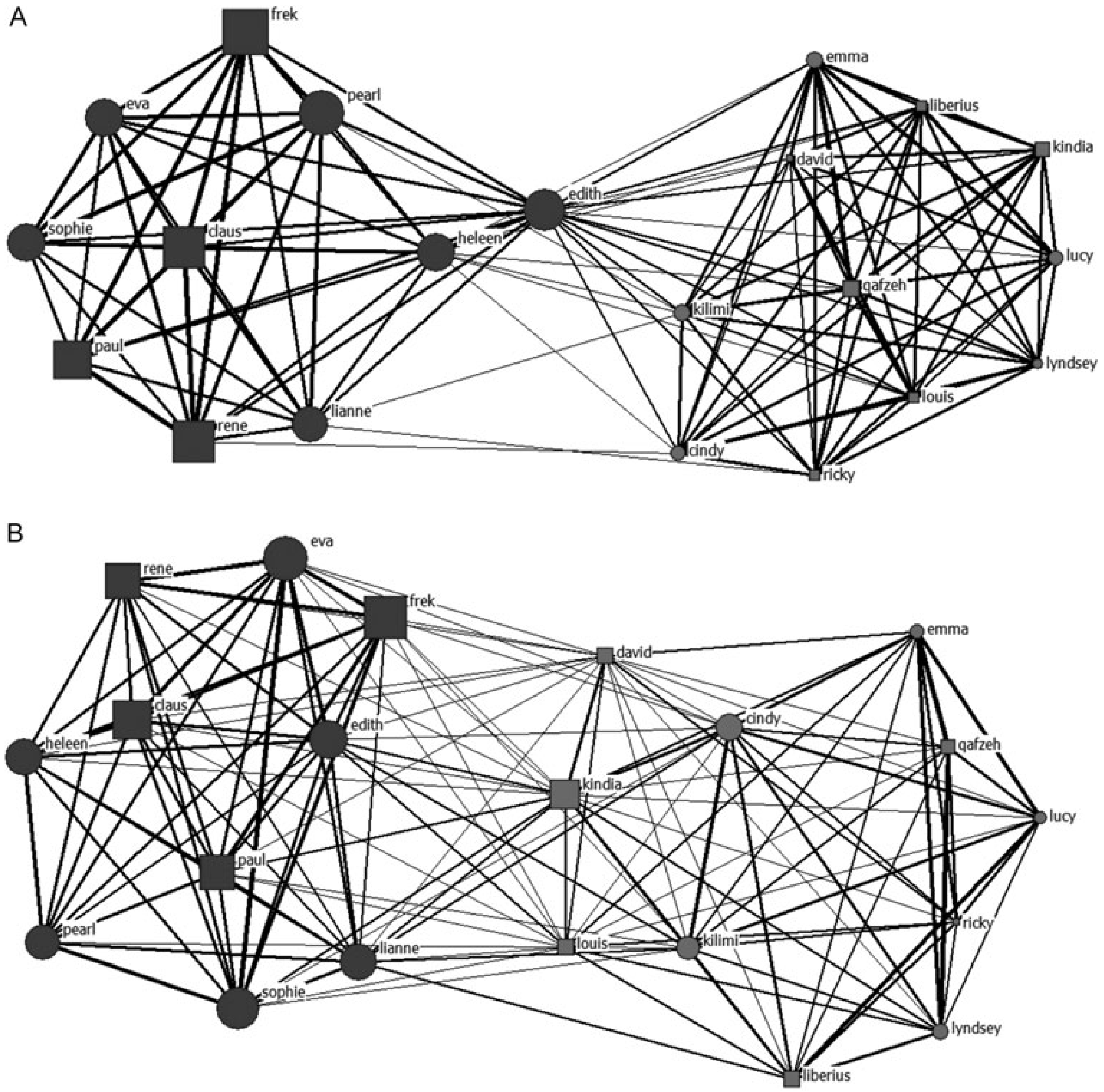


Fig. 5. Sociograms illustrating (A) association patterns from the early period (July to December 2010). (B) Association patterns from the late period (April to October 2011). Beekse Bergen chimpanzees are shown in dark grey; Edinburgh in light grey. Males are shown as squares and females as circles. The size of the node represents the eigenvector centrality index for the individual. Thickness of the link represents the strength of the association (associations below 5% are not represented). In the early period, the strongest cross-group associations were shown by Beekse Bergen member Edith, a 13-year-old estrus female, daughter of a central and established female, Eva. In the late period, the Edinburgh group member with the strongest cross-group associations was Kindia, a central 12-year-old male who was beginning to challenge for dominance in the Edinburgh group prior to integration.

related, so the association data mirrors the grooming data: significantly stronger associations developed between Edinburgh and Beekse Bergen individuals in the late period compared to the early period.

Despite all the indications that relations between Edinburgh and Beekse Bergen individuals have grown increasingly strong and affiliative in nature, the SNA still shows a clear and sustained existence of two subgroups determined by membership of the original two groups. We predict that the division between the subgroups will continue to break down, but the persistence and slow degradation of this division to date may also point to one of the reasons for the long-term success of this integration. The Budongo Trail facility is highly unusual in that it gives the chimpanzees the space and freedom to choose whom they associate with. This facility allows chimpanzees to express their natural fission–fusion social behavior and to use space to make active choices about whom to avoid and whom to

TABLE IV. Eigenvector Centralities of All Individuals in the Early and Late Periods

	Individual	Early	Late
Beekse Bergen	Claus	0.26	0.26
	Edith	0.26	0.26
	Eva	0.25	0.28
	Frek	0.27	0.27
	Heleen	0.25	0.25
	Lianne	0.24	0.25
	Paul	0.25	0.24
	Pearl	0.27	0.24
	Rene	0.26	0.24
	Sophie	0.25	0.27
Edinburgh	Cindy	0.18	0.21
	David	0.16	0.17
	Emma	0.19	0.16
	Kilimi	0.19	0.2
	Kindia	0.18	0.22
	Liberius	0.17	0.17
	Louis	0.17	0.17
	Lucy	0.18	0.15
	Lyndsey	0.17	0.17
	Qafzeh	0.19	0.16
	Ricky	0.17	0.13

associate with. This has allowed intergroup relationships to develop slowly. Our data indicate that after 16 months, although these chimpanzees can be viewed as a single community (low levels of aggression and the presence of affiliative behaviors between community members), the chimpanzees are still not choosing to form a single coherent group. Unsuccessful integrations may be due to spatial constraints forcing individuals to associate constantly from the first day; our data suggest that given the choice, building affiliative relationships with unfamiliar individuals is a considerably slower process.

Association patterns within the original groups were strong in the initial period and weakened over time. This mirrors findings of the maintenance of closer proximities between group members in squirrel monkeys and capuchin monkeys immediately following relocation to a new enclosure in Edinburgh Zoo [Dufour et al., 2011]. It seems that maintaining close proximity to known and trusted group members may aid individuals to cope when faced with uncertainty caused by either a new physical or a new social environment. Further, potentially supporting evidence for this comes from the tighter associations shown by the Beekse Bergen chimpanzees, compared to the Edinburgh chimpanzees. While both groups had to adjust to a new social environment, only the Beekse Bergen chimpanzees also experienced transportation followed by a new physical environment they had to adapt to: thus the uncertainty and stress facing the Beekse Bergen chimpanzees was arguably larger, and this may be reflected in their tighter association patterns. However, given that we do not have comparable social network data for the Beekse Bergen chimpanzees prior to their move, we cannot exclude the possibility that this group of chimpanzees has always been characterized by strong associations. Results indicated that both measures of association and overall grooming interactions between individuals of the same original group were stronger in the early period than the late period. This may indicate that they strengthened existing affiliative bonds as a mechanism to reduce stress and increase coping with their new social environment, supporting previous findings that strong social relationships can buffer individuals from potential negative effects of events such as physical relocations [Schaffner & Smith, 2005].

The analyses revealed that certain key individuals were important in facilitating between-group associations, with Edith from the Beekse Bergen group being particularly crucial in this role during the early period. At the time of integration, Edith, a nulliparous 13-year-old female, was at the age that her wild counterparts might leave their natal community to join a new one [Goodall, 1986], and thus she may have been particularly well suited to integrating and being accepted by an unfamiliar group. The integration of the two groups also seems to have changed the social role of Cindy in the Edinburgh group. Clark's [2011] data showed Cindy as a peripheral member of the group in 2009, with few associations or interactions, yet in our data Cindy appears well integrated and has a high centrality value, particularly in the late period, indicating she has shifted from a peripheral to a central role within her original group. Cindy's change in behavior may reflect an active adaptation to the new social situation, but it may also reflect a change of enclosure use with a reduced use of the bed areas once the Beekse Bergen group habitually used these areas. Long-term continuation of data collection in the community will allow us to track further changes in individual roles within the original groupings and enable us to examine this and other questions such as: Do individuals who integrate well with individuals from another group become ostracized or peripheralized to their original groups? Do well-integrated individuals become more or less dominant over time? In the future through the use of personality measures [Weiss et al., 2007], we may also be able to identify the personality profile of the individuals who have had a central facilitatory role in the long-term integration process.

SNA is a powerful tool and could be usefully applied to document the effects of births, deaths, changes in female cycling (e.g., from the insertion or removal of contraceptives implants in captivity), and integration of new individuals on the social structure of the captive study groups, as well as similar factors including immigration and emigration in wild populations. In captive settings SNA could be particularly helpful to inform management decisions, especially on the likely magnitude and nature of the effect that removing certain individuals would likely have on the social group [McCowan et al., 2008].

In conclusion, this study has documented the successful integration of two adult chimpanzee groups and has used SNA to chart key changes in the social networks of the integrated groups over time. Relationships between members of the different original groups have become significantly less aggressive and significantly more affiliative in terms of grooming and association. Despite this, over 1 year since successful integration, the presence of two distinct subgroups in the population is evident: chimpanzees are still maintaining stronger relationships with more familiar individuals from their original groups, indicating that when given the space to choose whom to associate and interact with, full integration with unfamiliar individuals is likely to be a very lengthy process.

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