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Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees

Abstract Handclasp grooming is a unique social custom, known to occur regularly among some, but not all populations of chimpanzees (*Pan troglodytes*). As with other cultural behaviors, it is assumed that this distinctive grooming posture is learned socially by one individual from another. However, statistical comparisons among factors thought to influence how a behavior spreads within a group have never, to our knowledge, been conducted. In the present study, the origination and spread of handclasp grooming in a group of captive chimpanzees was followed throughout more than 1,500 h of observation over a period of 12 years. We report on the frequency, bout duration, and number and demography of performers throughout the study period, and compare these findings to those reported for wild populations. We predicted that dyads with strong affiliative ties, measured by time spent in proximity to and grooming one another, were likely to develop a handclasp grooming partnership during the study period. A quadratic assignment procedure was used to compare correlations among observed frequencies of grooming and proximity with handclasp grooming in all possible dyads within the group. As predicted, the formation of new handclasp grooming dyads was positively correlated with the rate of overall grooming and proximity within a dyad. In addition, in nearly all dyads formed, at least one individual had been previously observed to handclasp groom. We concluded that affiliation and individual experience determines the transmission of handclasp grooming among captive chimpanzees.

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Introduction

Most of the socially learned behavior that has been documented in nonhuman primates relates to interactions with the physical environment, such as tool use, foraging techniques, and other behaviors often labeled "material culture" (Nakamura 2002). However, a small number of "social conventions" (cf. Perry et al. 2003b) also exist. These include unique grooming patterns such as social scratching (Nakamura et al. 2000) or leaf-clipping in chimpanzees (*Pan troglodytes*; Boesch 1996; Nishida 1987; Whiten et al. 1999), and hand-sniffing and various "games" among wild white-faced capuchin monkeys (*Cebus capucinus*; Perry et al. 2003a, b). Apart from these social conventions, the transmission of social "attitudes" such as peacefulness (e.g., de Waal and Johanowicz 1993; Sapolsky and Share 2004), and social positions, such as the inheritance of social rank in cercopithecine monkeys (e.g., Kawai 1958; Kawamura 1958) and the transmission of preferred social partners from mothers to daughters (de Waal 1990, 1996), have also been reported.

One social custom that has attracted significant attention is handclasp grooming in chimpanzees. First reported from Mahale Mountains National Park, Tanzania, by McGrew and Tutin (1978) this striking behavior is known to be customary in some, but certainly not all, wild populations (McGrew et al. 2001; Nakamura 2002; Whiten et al. 1999). The handclasp grooming posture has also been well documented in one captive chimpanzee group housed at the Field Station of the Yerkes National Primate Research Center, near Atlanta, Georgia (de Waal and Seres 1997). A second group at the Yerkes Field Station, kept under almost identical conditions as the first, has never been observed to handclasp groom despite equally intensive

observation. The chimpanzees in each group must be equally able to physically perform the posture, but ecological, functional, or methodological variants cannot explain with any certainty why handclasp grooming is present in one group, but absent in another.

The widely accepted explanation for the occurrence of handclasp grooming and other cultural behaviors is that individuals within a population adopt new social customs by watching and interacting with members of their group. The question of how behaviors are transmitted from one individual to another can be addressed on at least two different levels. One method is concerned with identifying the particular learning mechanism through which behaviors are transmitted, such as imitation, emulation, local, and stimulus enhancement (e.g., Whiten 2001; Whiten and Ham 1992). Although this approach is widely applied in a range of taxa, establishing the mechanism via which learning takes place has historically proven to be an arduous task requiring controlled experimental settings. A complementary, equally important, issue is not how, but from whom a behavior is learned.

Traditionally, this issue has been addressed with observational methods. Among Japanese macaques (*Macaca fuscata*), for example, the practice of sweet-potato washing spread first within the innovator's family and to her peers, and was only later adopted by others (Hirata et al. 2001; Kawai 1965). Similarly, Perry et al. (2003a, b) reported that among wild white-faced capuchin monkeys, games and other social customs appeared to spread along affiliative lines. Nevertheless, reports rigorously examining the spread of behavioral variations within a population are rare. There are a few notable exceptions in which the transmission pattern of a cultural behavior has been illustrated and/or described (e.g., Hirata et al. 2001; Lonsdorf et al. 2004; Matsuzawa et al. 2001; Perry et al. 2003b), but thus far all such reports lack statistical evaluation of the data against a random model. As a result, questions about the probability that some individuals, but not others, acquired a particular new behavior remained unanswered.

The relative absence of rigorous analysis may be attributed in part to challenges of establishing the innovation and diffusion of a particular behavior within a population (McGrew 1998). Doing so is difficult in natural settings, as behavioral traditions are often noticed long after the tradition has been established. Moreover, rough terrain, thick foliage, and other environmental challenges inherently limit when and how these behaviors are observed by human researchers. Finally, chimpanzee communities have a fluid composition, such that as individuals immigrate and emigrate and groups fissure and fuse the diffusion of a behavior within a particular community can be difficult to follow. Therefore, the spontaneous emergence of handclasp grooming within the Yerkes group provided a unique opportunity in that the transmission of the behavior from one individual to another, since its origination, could be closely followed in a contained group for many years.

There are a number of reasons why affiliation might be an important factor in the development of handclasp grooming within a dyad. First, social grooming in general represents an intimate affiliative interaction between two individuals (McGrew and Tutin 1978). Moreover, handclasp grooming requires at least some degree of cooperation, coordination, and trust among the grooming partners (de Waal and Seres 1997). Therefore, we would expect that only pairs with strong affiliative ties would establish a handclasp grooming partnership. Affiliation can be defined on a number of levels, from genetic relatedness to complex political alliances. It can also be measured in terms of the amount of time two individuals spend in proximity to one another or in engaged in positive interactions such as grooming.

The purpose of the present study was twofold. Our first goal was to document the continued spread of handclasp grooming throughout the Yerkes group in terms of the number of individuals performing it, the rate at which it occurs, the duration of handclasp grooming bouts, and the variety and composition of handclasp grooming dyads. This goal expands upon the findings reported by de Waal and Seres (1997). Secondly, we sought to evaluate retrospectively which factors may have promoted the spread of this social custom. Specifically, we investigated how two variables—previous experience with the behavior and affiliation—might have affected the formation of new handclasp grooming dyads. We were able to conduct such an analysis thanks to more than a decade of continued data collection on behavior in this particular group with unchanged methods of observation.

Methods

For the past 12 years (1992–2003), handclasp grooming has been observed in one of the two socially housed groups of chimpanzees at the Yerkes Field Station in Lawrenceville, Georgia. During this period, the colony was comprised of between 16 and 19 individuals. A description of all subjects can be found in Table 1. Group composition varied slightly during the study due to the birth of six infants, several temporary removals for veterinary reasons, and the permanent removal of four individuals for management purposes. With the exception of an adult male who was introduced into the colony in 1991, all individuals had been living together for up to 15 years prior to the study's onset or were born into the group (see de Waal and Seres 1997, for more details).

The chimpanzees have access to indoor sleeping quarters and a large outdoor compound, measuring 750 m^2. The compound is equipped with visual barriers, vertical climbing structures, plastic barrels, large tires, and an assortment of toys and other objects with which the chimpanzees can interact.

Table 1 Composition of the study group of chimpanzees (*Pan troglodytes*) at the Yerkes Field Station

Subject	Sex	D.O.B.	D.O.R.	First HCG
Jimoh[a]	M	01/01/1964[b]	09/11/1996	1992
Marilyne[a]	F	01/13/1971	11/30/1993	
- Reinette	F	12/17/1987		1993
Gwennie[a]	F	01/11/1969	03/18/1999	
- Socrates	M	01/23/1987		1995
- Claus	M	12/25/1992		
Mai	F	01/01/1964[b]		1992
- Natasha	F	12/19/1987	02/23/2004	1995
- Missy	F	07/08/1993		
Borie	F	01/01/1964[a]		1992
- Georgia	F	08/27/1980		1992
- -Cathy	F	10/05/1989		1998
- -Liza	F	03/19/1994		
- Rita	F	07/23/1987		1993
- -Tara	F	09/05/1995		2002
Atlanta	F	08/10/1965	12/21/2000	1997
- Rhett	M	04/20/1989		1998
Peony	F	01/01/1968		1992
- Anja	F	01/09/1980		1993
- -Bjorn	M	07/16/1988		1994
- Dona	F	04/03/1990		1999
- Azalea[a]	F	03/07/1987		

M male, *F* female, *D.O.B.* date of birth, *D.O.R.* date of removal or death, *HCG* handclasp groom, all dates are month/day/year. Off-spring of females are indicated by a dash to the left of subject's name (e.g., Reinette is the daughter of Marilyne)
[a]Individual not included in quadratic assignment procedure analysis
[b]Approximate date of birth

All handclasp grooming bouts observed by the authors, research technicians, and other members of our team were recorded. All researchers were familiar with, and could accurately identify, the chimpanzees and the handclasp grooming posture. Handclasp grooming was recorded whenever it occurred, with the records including the date of observation, the identity of the individuals involved, and the duration (in seconds) of the clasping posture. The majority of data were collected by trained research technicians during 90-min observation sessions (described in detail by de Waal 1989) during which the group did not have access to the indoor sleeping quarters and could be observed without obstruction from a tower located at one corner of the outdoor compound. Scan samples of state behavior patterns were taken at regular intervals (every 5 min through 1993 and every 10 min in the years thereafter), while point events (e.g., aggression, mating, and vocalizations) were also noted. Four state behaviors—i.e., contact sitting, sitting within arm's reach, grooming, and mutual grooming—collected during scans were used to measure the overall affiliation between dyads in our analyses.

Observations were conducted with regularity (approximately 1/week) from January 1992 to June 2000 and again from January 2002 to December 2003. No observations were made in the year 2001. In total, the colony was observed for 1,525 h over 11 years, and in any one year the number of total observation hours ranged from 48 to 348. The majority of handclasp grooming bouts (i.e., 82.3%) were observed during these controlled observation sessions.

For each year of study, a dyadic matrix was created for two social variables, grooming and proximity. Grooming was defined by the percentage of scan samples during which a dyad was seen grooming, and proximity was defined as the percentage of samples during which individuals were merely sitting in contact or within arms' length. These two measures were behaviorally independent as individuals could be doing only one at the time a scan was completed. For each dyad, a single score for each variable was calculated by taking the mean over the years in which the dyad was present. For dyads that developed handclasp grooming, the measure was limited to the years leading up to but not including year in which the first handclasp occurred. As a result, we had measures for average grooming and proximity for each dyad. A matrix for handclasp grooming was also created. Handclasp grooming was binary, with a value of 1 assigned to dyads observed to handclasp groom, and 0 to those that did not. All three matrices were symmetrical, that is, one value applied to both dyadic directions.

Results

Rate

Since 1992, 293 handclasp grooming bouts have been observed at the Yerkes field station. Of these, 241 bouts were observed during a scheduled observation session. For each study year, the rate of handclasp grooming was determined by dividing the number of bouts observed by the total hours of observation in that year (Fig. 1). The hourly rate of handclasp grooming bouts increased over the course of the study period from approximately 1 every 28 h (0.036/h) in 1992 to just less than 1 every 2 h (0.472/h) in 2003. Hourly rate correlated positively with the year of study (Pearson $r = 0.96$, $n = 241$, $p < 0.001$).

Duration

Duration was recorded for all instances in which both onset and termination of the handclasp grooming bout was observed ($n = 236$). Overall, the duration of individual bouts varied greatly throughout the study period, from only a few seconds to several minutes. The longest bout continued without interruption for 480 s (8 min), and involved two adult females, Georgia and her daughter Cathy. Five additional pairs were observed to maintain the posture at least once for over 5 min. The median duration (in seconds) of handclasp grooming bouts in each year are presented in Fig. 2. As reported by de Waal and Seres (1997), from 1992 to 1996,
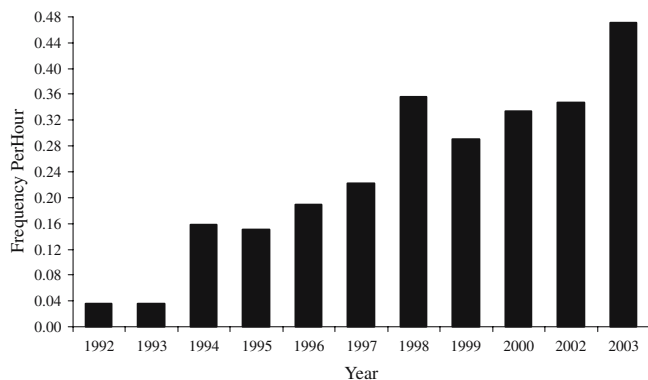
Fig. 1 Frequency, per hour of observation, of handclasp grooming bouts bychimpanzees (*Pan troglodytes*) observed from 1992 to 2003. The rate of handclasp grooming increased significantly throughout the study period
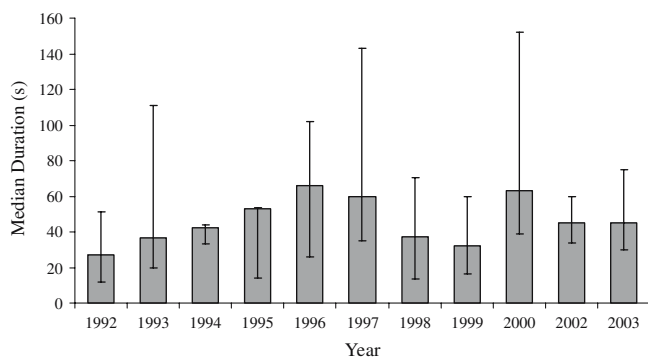

Fig. 2 Median duration (in seconds) of handclasp grooming bouts (*error bars* = interquartile range) observed from 1992 to 2003

duration increased with year of study, but this effect disappeared when all 12 years were considered (Spearman $r = 0.099$, NS). Across all years, handclasp grooming bouts had a median duration of 45.0 s (interquartile range 20–33.5 s) and a mean duration ($\pm$SD) of 66.6 ± 71.4 s.

Performers

Handclasp grooming was believed to originate with a single adult female, Georgia (de Waal and Seres 1997), as she was involved in all 12 handclasp grooming bouts observed in the first study year. Including Georgia, 16 individuals (4 males and 12 females) were observed to handclasp groom at least once during the entire study period (Table 1). Among them, 9 were immature (ages 5–9) and 7 were adults (10 years or older) at the time of their first observed handclasp grooming bout. The youngest observed performers, both females, were 5 years 11 months (Reinette) and 5 years 9 months (Rita) old when their first handclasp was observed. Both individuals first performed the posture with the same adult female, Peony, to whom neither is related. Rita subsequently became the most active performer in the

colony as she was involved in 45.1% (132 of 293) of all observed handclasp grooming bouts.

Six individuals, 1 male and 5 females, within the colony were never observed to handclasp groom. Although some of these individuals were born during the study period, they all reached the age of 5 years old, the youngest age at which the handclasp grooming has been observed in any chimpanzee group, at least 1 year prior to the end of the study. Therefore, their absence of handclasp behavior is not thought to be a function of age.

Dyadic demographics

The 16 individual performers each partnered with between 1 and 11 different individuals to create 48 unique handclasp grooming dyads. However, dyads contributed far from equally to the rate of handclasp grooming, in that the frequency of handclasp grooming bouts observed per dyad during the study period ranged from 1 to 70. The most active dyad, a mother–daughter pair, were observed to handclasp groom in all but the first year of the study period, and performed 24% (70 of 293) of all observed handclasp grooming bouts.

The composition of the dyads varied with respect to both the sex and age of the individual performers. Of the 48 dyads observed to handclasp groom, 3 involved two males, 30 involved two females, and 15 one male and one female. These frequencies reflect 33%, 19%, and 31% of total number of possible dyadic pairings of each of these sex categories, respectively. The method for determining the total number of possible dyads is described in the next section. Across sex categories the ratio between dyads that did and did not handclasp groom did not differ significantly ($\chi^2 = 3.48$, $df = 2$, NS).

With respect to age, adults (10 years of age and older) most often partnered with another adult in the handclasp grooming posture (Fig. 3). However, immature individuals (individuals between 5 and 9 years of age) were also observed to handclasp groom, and were involved in 90 of the 293 (30.7%) observed handclasp grooming bouts. Although in most instances, the immature individual performed handclasp grooming with an adult, nine handclasp grooming bouts between two immature individuals were also observed. Eight of these bouts were performed by two females, Rita and Reinette; and on one occasion Rita was observed to handclasp groom with Bjorn, a young male. Rita and Reinette had each performed handclasp grooming with adult partners prior to their pairing. However, for Bjorn, the first observed handclasp was with another immature individual.

Available dyads

In the Mahale chimpanzee community, the number of dyadic grooming combinations was described as being
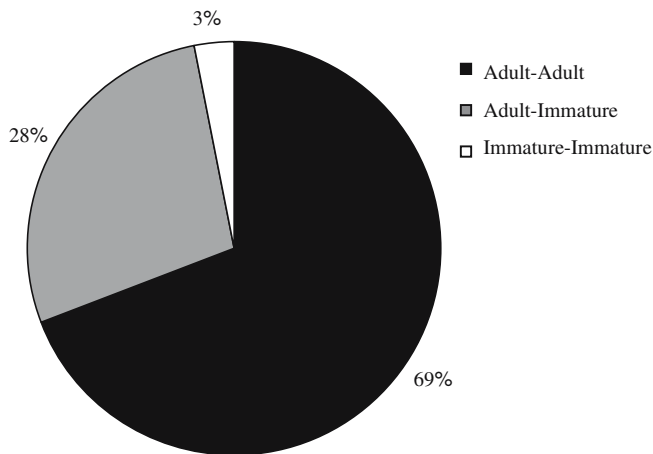
Fig. 3 Proportion of total handclasp grooming bouts ($N = 293$) performed by dyads of differing age compositions; Adult ≥10 years old, Immature 5–9 years old

"relatively" small compared with the number of available dyads (Nakamura 2002). With this in mind, we were interested in examining to what extent dyadic combinations of individuals within the Yerkes colony were observed to handclasp groom. We defined the number of available dyads in the following manner.

For each study year, we considered that individuals that were present for any portion of that year could partner with any other individual present in that same year in a handclasp grooming dyad. For example, among individuals A, B, and C, three unique dyads could be formed: A with B, A with C, and B with C. However, we considered 5 years to be the earliest possible age at which an individual could perform this grooming posture. Accordingly, individuals less than 5 years old as of January 1st of a given year were excluded. Finally, dyads were symmetrical, in that pairing A with B is identical to B with A, and thus each dyad was counted only once. Based on these criteria, a total of 211 unique dyadic combinations were available throughout the study period. The dyads observed to perform the handclasp grooming posture ($n = 48$) therefore represent only 22.7% of all available pairs as defined here.

It follows that, in any given year, the number of new dyads observed to handclasp groom was likely to be significantly less than the number of new available dyads. Thus, we examined the data longitudinally, beginning with the second year of study (the year 1993). In doing so, we found that the number of new available

dyads varied greatly because individuals were removed for management reasons or were added to the list of potential handclasp groomers if their age exceeded 5 years. In addition, we assumed that once a dyad was observed to handclasp groom, that dyad continued to handclasp groom, even though we may not observe it to do so. As a result, we were able to evaluate, for each year, the number of new dyads observed to handclasp groom as a proportion of all available new dyads (Table 2). In most years, the proportion of newly formed handclasp grooming dyads was strikingly low, i.e., less than 5% of available new dyads. At its peak, in 1999, 12% of available dyads formed handclasp grooming pairs. The limited spreading of the pattern raises the question which factors decide which dyads will develop handclasp grooming.

Previous experience

Prior performance of the handclasp grooming posture by one or both partners may be a good predictor of the formation of a new dyad among individuals aged 5 years and older. For each study year, we tallied the number of new dyads formed, and categorized each new dyad on the basis of whether one, both, or neither individual had been observed to handclasp groom with another partner in prior years. Experience was a binary (yes or no) measure based on whether an individual had been observed to handclasp prior to the given year regardless of frequency. The findings are summarized in Table 3. For each study year, the number of new dyads in which neither individual, or one or both individuals had been observed to handclasp groom in a prior year, are reported. Although at least two new dyads were observed in every study year, during the entire study only one new dyad formed from two previously inexperienced individuals. After the first study year, in 97.7% of 44 new dyads at least one individual had performed handclasp grooming in a previous year.

Measures of affiliation

Data from observations made throughout the study period were used to test the hypothesis that individuals that were often seen grooming or sitting in contact with one another were more likely to develop handclasp grooming at some point during the study period. Seventeen individuals, part of 153 dyads, were included in the following analysis. Four individuals were excluded.

Table 2 Proportion of potential new handclasp grooming dyads that formed in each year of study

	1993	1994	1995	1996	1997	1998	1999	2000	2002	2003
New dyads	5	4	2	2	2	4	12	5	6	2
Available dyads	64	68	92	105	80	101	98	102	98	109
New/available	0.08	0.06	0.02	0.02	0.03	0.04	0.12	0.05	0.06	0.02

Table 3 Experience of individuals in dyad

Year	Neither (n)	One (n)	Both (n)
1993	1	4	0
1994	0	2	2
1995	0	2	0
1996	0	0	2
1997	0	1	1
1998	0	2	2
1999	0	2	10
2000	0	0	5
2002	0	2	4
2003	0	0	2
Total	1	15	28

For each study year, the number of new dyads observed in which neither one or both individuals had been observed to groom with other partners in a previous year

Fig. 4 Proportion of dyads categorized within top 25%, middle 50%, and lowest 25% of grooming and proximity scores which were observed to handclasp groom during the study period

A female, born in 1987, met the 5-year age limit only for one full year of the study period. The remaining three individuals were removed from the colony in 1993, 1996, and 1999, respectively. Excluding these individuals fulfilled the requirement for the present matrix analysis that no empty cells exist.

The grooming and proximity matrices (described in Methods) were each correlated with the handclasp grooming matrix using a quadratic assignment paradigm developed by Dow and his colleagues (Dow and Cheverud 1985; Dow et al. 1987) and applied to primate behavior by Dow and de Waal (1989) and de Waal (1991). The model compares the Pearson coefficient for each pair of matrices (i.e., the grooming and handclasp matrices, and the proximity and handclasp matrices) with a distribution generated by random permutations of the same matrices. We performed 5,000 permutations per comparison; therefore, the smallest possible one-tailed probability of an observed correlation is 0.0002.

When all dyads are considered, both grooming and proximity were found to correlate positively with the chance that this dyad would develop handclasp grooming. The correlation with grooming rate was $r = 0.269$, $p < 0.001$, and the correlation with proximity was $r = 0.427$, $p < 0.001$. To illustrate this finding, we placed each dyad into one of three categories—the top 25%, middle 50%, and lowest 25%—according to the distribution of the grooming and proximity scores of all dyads. Figure 4 shows the proportion of dyads within these three categories which were observed to handclasp groom during the study period.

Discussion

Handclasp grooming is a unique social custom, known to occur regularly within some, but not all, communities of chimpanzees. This behavior meets the criteria of a cultural pattern, as defined by Kroeber (1928) and adapted by McGrew (1998) in that we observed (1) the invention of novel pa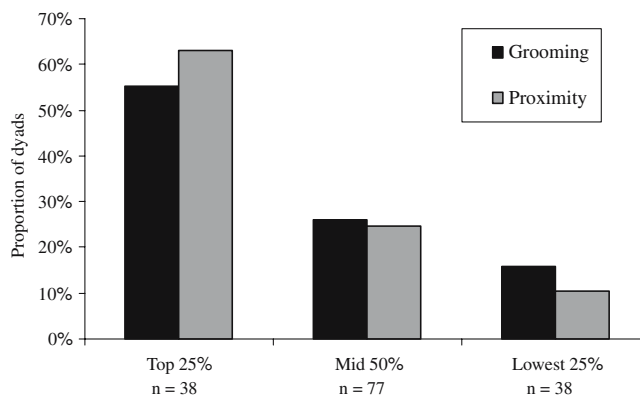ttern of behavior, (2) transmission across family and other social units, (3) persistence of the pattern in the absence of the originator (de Waal and Seres 1997), and (4) endurance across generations. In addition, the expansion in number of performers over time could not possibly be attributed to either genetic transmission (McGrew and Tutin 1978; Whiten et al. 1999) because transmission spread both horizontally and vertically between non-related individuals, or ecological explanations as the behavior is absent in a second group kept under nearly identical conditions.

Although patterns of social transmission have been described for other cultural behaviors in nonhuman primates, the present study is the first to statistically connect social affiliation and the spreading of a new behavior. The proportion of time dyads spent in proximity to each other correlated positively with the development of handclasp grooming. The amount of grooming in a dyad had the same effect, but less pronounced than mere association. These findings support the Bonding- and Identification-based Observation Learning (BIOL) model (de Waal 2001) which predicts transmission biased by social affiliations. The spreading of handclasp grooming also seems to support BIOL's claim that social learning does not necessarily require reward (see also Bonnie and de Waal 2004). It is hard to see what rewards individuals may reap from handclasp grooming. The behavior's social or hygienic function is unclear, although it has been speculated that the posture promotes reciprocity in grooming and can, in fact, be used to *symbolize* close relationships. Thus, de Waal (2001, p.250) describes how an adolescent male returning after a lengthy absence to the Yerkes group was welcomed by an unusual succession of handclasp grooming with a variety of partners as if to confirm that he "belonged."

Learning from others requires proximity and attention to their behavior (Coussi-Korbel and Fragaszy 1995; van Schaik 2003; van Schaik et al. 2003), and it is likely that the development of handclasp grooming by an individual is influenced by social affiliations. Nevertheless, we cannot rule out the possibility that individual

learning acts within an individual's social experience to promote acquisition of a novel behavior. Experience is one factor that seems to affect the formation of new handclasp grooming dyads, such that previous participation in the pattern with others seems a key factor. We observed only one new handclasp grooming pair in which both individuals had never before been observed to handclasp groom with another partner. Possibly, both individuals had learned the behavior from watching others, but we cannot of course rule out that one or both had in fact participated in handclasp grooming when we were not there to see it. The most likely possibility is the kinesthetic learning pointed out by de Waal and Seres (1997). Initially, naïve individuals gain proprioceptive feedback while participating in handclasp grooming with an experienced partner, and then translate this into handclasp grooming with others.

Although handclasp grooming has been observed in at least seven different wild communities (Nakamura 2002; Whiten et al. 1999), detailed descriptions of the behavior exist for only two study groups, both at Mahale Mountains National Park, in Tanzania. Compared with these wild populations, handclasp grooming among Yerkes chimpanzees differs on several levels. First, the rate of handclasp grooming per observation hour among the Yerkes chimpanzees was initially less than either the M- or K-groups of Mahale (McGrew and Tutin 1978; Nakamura 2002). However, the rate of handclasp grooming at Yerkes increased steadily throughout the study period, and by 2003 was more than twice that of the M-group, but only slightly higher than that of the neighboring K-group. Similarly, individual handclasp grooming bouts typically lasted longer at Yerkes than among either group at Mahale, where the longest reported bout of 296 s is significantly less than the longest bout observed among the Yerkes chimpanzees.

With respect to age, the youngest individuals at Yerkes observed to handclasp groom (5 years 9 months and 5 years 11 months, respectively) were only slightly older than the youngest groomers among wild populations (5 years 4 months and 5 years 8 months, as reported by Nakamura 2002). Whereas in the wild, both these young individuals performed the posture first with their mother, the Yerkes chimpanzees generally partnered with unrelated adult females. In addition, on multiple occasions, immature individuals at Yerkes were observed to engage in handclasp grooming with each other. This has never been reported for wild populations (Nakamura 2002).

Finally, in all three wild communities studied by Nakamura (2002), most adult males performed the behavior, whereas only half of the females did. However, unlike the Mahale M-group, in which two adult males were the most frequent grooming partners, at Yerkes the originator of the behavior and subsequently its most active performers were all female. In terms of dyad formation, McGrew and Tutin (1978) reported that K-group dyads tended to be of mixed sex composition, and it was later reported that in this group handclasps never occurred between two females (Nakamura 2002). In contrast, handclasp grooming between two females accounted for 36.8% of observed bouts in M-group (Nakamura 2002) and 81.6% at Yerkes. This is partly due to the preponderance of females in our group; however, if the number of available dyads is considered, handclasp grooming was not significantly associated with a particular sex class combination in the Yerkes group.

It is possible that the patterns emerging among the Yerkes chimpanzees are a product of different social or ecological demands of captive versus wild environments. For example, the Yerkes colony is a contained, stable social group that has been kept together, with limited disruption, for many years. Most individuals were born into and have remained in the group into adulthood, and as a result, there has been significant time for longstanding, trusting relationships to be formed. It is well known that, compared to wild communities, female chimpanzees in captive colonies develop much closer ties (de Waal 1994), which may be reflected in the handclasp distribution in our group. In addition, captive apes receive daily food provisioning, and unlike wild populations therefore do not need to spend long hours foraging. As a result, the Yerkes chimpanzees have more time for grooming. Each of these factors may have enhanced the spreading of a social custom within the Yerkes colony.

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