Report

Current Biology

Distribution of a Chimpanzee Social Custom Is Explained by Matrilineal Relationship Rather Than Conformity

Highlights

- Individuals within a chimpanzee group vary widely in grooming style
- Adult chimpanzees retain their mother's grooming styles
- Chimpanzees do not conform to the grooming style of the social community

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In Brief

Palm-to-palm clasping is a form of mutual grooming that varies in frequency among chimpanzee social groups. Wrangham et al. find that individuals conform in their grooming styles only to their mothers, not to the larger group.

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Distribution of a Chimpanzee Social Custom Is Explained by Matrilineal Relationship Rather Than Conformity

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SUMMARY

High-arm grooming is a form of chimpanzee grooming in which two individuals mutually groom while each raising one arm. Palm-to-palm clasping (PPC) is a distinct style of high-arm grooming in which the grooming partners clasp each other's raised palms. In wild communities, samples of at least 100 observed dyads grooming with raised hands showed PPC frequencies varying from <5% (M group, Mahale) to >30% dyads grooming (Kanyawara, Kibale), and in a large free-ranging sanctuary group, the frequency reached >80% dyads (group 1, Chimfunshi) [1, 2]. Because between-community differences in frequency of PPC apparently result from social learning, are stable across generations, and last for at least 9 years, they are thought to be cultural, but the mechanism of transmission is unknown [2]. Here, we examine factors responsible for individual variation in PPC frequency within a single wild community. We found that in the Kanyawara community (Kibale, Uganda), adults of both sexes varied widely in their PPC frequency (from <10% to >50%) and did not converge on a central group tendency. However, frequencies of PPC were highly consistent within matrilines, indicating that individuals maintained lifelong fidelity to the grooming style of their mothers. Matrilineal inheritance of socially learned behaviors has previously been reported for tool use in chimpanzees [3] and in the vocal and feeding behavior of cetaceans [4, 5]. Our evidence indicates that matrilineal inheritance can be sufficiently strong in nonhuman primates to account for long-term differences in community traditions.

RESULTS AND DISCUSSION

Hand-clasp grooming was originally defined as a form of mutual grooming in which each partner holds his or her hand above the head while clasping the other's raised hand, wrist, or arm [6]. However, the term "hand-clasp grooming" has become inappropriate because it has been used to include all cases in which two groomers hold their arms high and in physical contact, regardless of whether there is any clasping (Figure 1). To reduce confusion, we use the term "high-arm mutual grooming" ("high-arm grooming" for short) for episodes of mutual grooming when two partners sit facing each other, each holding an elbow higher than either of their shoulders, and their raised hand, wrist, or arm is touching the similarly raised hand, wrist, or arm of the partner. In 3 of 11 wild populations, high-arm grooming is absent, suggesting that elsewhere it is socially learned [7] (see Supplemental Information). In support of social learning, the western and eastern sub-species each include at least one population in which the pattern is present and at least one in which it is absent [7]; high-arm grooming has been observed to be socially propagated in captivity [8]; and wild mothers sometimes mold their young offspring's high-arm grooming behavior [9].

Within communities that practice high-arm grooming, there is little evidence of variation in how often individuals use it. However, substantial variation has been reported in the style of grooming used. Following McGrew et al. (2001), we define a "palm-to-palm clasp" (PPC) as the sub-category of high-arm grooming in which the hands are clasped with mutual palmar contact (Figure 1A) [10]; and %PPC is the proportion of an individual's high-arm grooming bouts featuring PPC. Our aim is to

Figure 1. Styles of High-Arm Grooming

(A) Palm-to-palm clasp (PPC) (photo by Suzi Eszterhas, used with permission). (B) Forearm-to-forearm contact (photo by Andrew Bernard, used with permission).

Types of contact of upper arms include diverse combinations of hand, wrist, and arm. Arms can be straight or bent. Panel (B) illustrates why the term "high-arm grooming" is more appropriate than "hand-clasp grooming."

understand how and why individuals vary in their tendency to use PPC during high-arm grooming.

We studied chimpanzees in the Kanyawara community of Kibale National Park, western Uganda. Observations were approved by the Institutional Animal Care and Use Committee at Harvard University (protocol 96-03). All adults engaged frequently in high-arm grooming (Table S1), and all also sometimes performed PPC, albeit with varying frequency (Table S2). In 2011–2015, a total of 35 members of the Kanyawara community were photographed in 932 independent bouts of high-arm grooming. Unless stated otherwise, we restricted analysis to the 18 individuals for whom at least 40 episodes of high-arm contact grooming were photographed and for which both raised hands were intact (mean ± standard deviation = 76.5 ± 28.6 per individual, range 42–128). Across individuals, %PPC ranged from 6.8% to 57.8% (mean ± standard deviation 32.6% ± 18.9%).

One hypothesis for the distribution of PPC values is that individuals would show conformity, defined as adopting the preferred strategy of the majority of group members [11]. In accordance with the conformity hypothesis, we would predict a single peak of values. In contrast to this expectation, individual %PPC values were distributed bimodally, peaking in the ranges of 0%–20% and 40%–60% PPC, either side of the median value of 35.1% (Figure 2). Given that chimpanzees are male philopatric and have therefore spent their lives in this community, whereas most females immigrate as adolescents, the conformity hypothesis suggests that adult males would have a more centralized tendency than females. However, Figure 2 shows that males varied widely, with no evidence of a sex difference in variance. To find out whether duration of exposure to the group influenced %PPC, we examined whether younger individuals or more recent immigrants had %PPC values that were furthest from the group median. We found no correlation between number of years of exposure to the group (from age 10 onward) and difference between an individual's %PPC score and the group median (Pearson $r = 0.14$, $n = 18$, p not significant [ns]). In sum, we found no evidence that individuals converged in their frequencies of PPC.

We therefore considered factors that might explain individual variation in %PPC. Males spent a higher proportion of time engaged in high-arm grooming than females did (median number of minutes per day in high-arm grooming: males 2.1, $n = 16$ individuals; females 0.7, $n = 16$; Mann-Whitney $U = 25$, $z = 3.86$, $p < 0.001$). However, because this sex difference was due entirely to a sex difference in the rate of mutual grooming, it had no impact on %PPC. First, the rate of high-arm grooming as a percentage of all mutual grooming did not differ between females and males (females 44.9% ± 25.9%, $n = 16$; males 48.8% ± 17.9%, $n = 16$; Mann-Whitney $U = 89.5$, $z = 0.93$, p ns; Table S1). Thus, the sex difference in time spent in

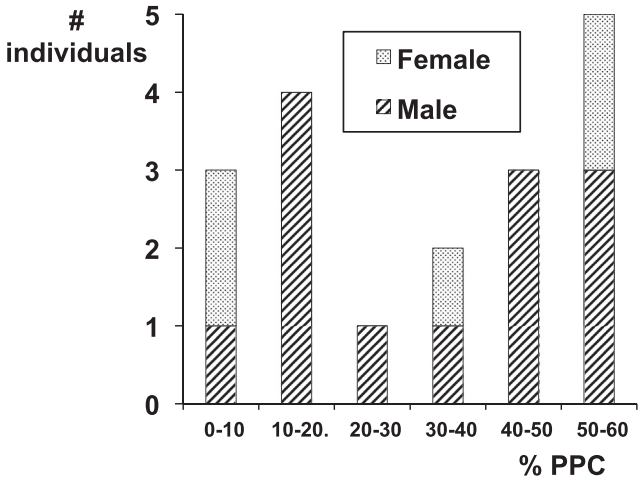

Figure 2. Individual Differences in Frequency of PPC within the Kanyawara Community

%PPC = percentage of high-arm grooming episodes in which the individual exhibited PPC. Median for the population was 35.1. All adolescents and adults in the community were habitual high-arm groomers (Table S1), during which they sometimes groomed with hands clasped palm-to-palm (Table S2). Individuals shown are all those with at least 40 photographs recording hand position during high-arm grooming. The five females shown include: 0%–10% OU (resident for >15 years since immigrating in 1993) and OT (OU's daughter, resident since her birth in 1998); 30%–40% TG (resident for >14 years since immigrating in 1994); 50%–60% AL (resident for >13 years since immigrating in 1995), LR (LP's daughter, resident since her birth in 1989). Tables S1 and S2 show data in full.

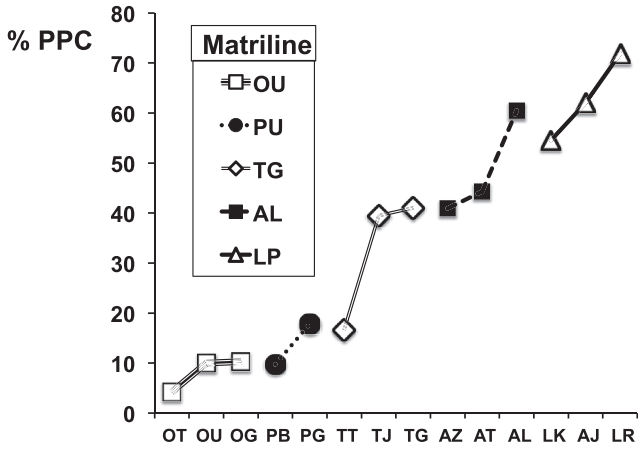

Figure 3. PPC Frequency by Matriline

Y axis shows %PPC in high-arm grooming episodes. Data are shown for all 14 independent individuals in the Kanyawara community with known matrilineal relationships and >40 photographic records of high-arm grooming. Matrilines: OU immigrant mother, OG son, OT daughter; PB, PG sons of mother PU who died in 2003; TG immigrant mother, TJ, TT sons; AL immigrant mother, AT, AZ sons; AJ, LK sons, LR daughter of mother LP (who died in 2004). Note that OT and LR remained in their natal community as adults.

high-arm grooming was explicable entirely by a sex difference in rates of mutual grooming. Second, %PPC did not differ between males and females (male mean 32.0% ± 17.3%, n = 13; female 34.1% ± 24.7%, n = 5; Mann-Whitney U = 31, z = 0.099, p = 0.92; Table S2). There was also no relationship between % PPC and age (r = 0.03, n = 18, p ns, range 9–~58 years; Table S2). Thus, %PPC was not related to either sex or age.

A higher tendency for PPC could in theory result from some individuals being more motivated to engage in high-arm grooming. To test this idea, we indexed motivational strength by two factors that might relate positively to the intensity of interest in grooming, i.e., the proportion of time spent in high-arm grooming and the duration of episodes of high-arm grooming. First, among individuals with at least 10 hr of focal observation for every hour of the day from 0700h to 1800h, there was no relationship between the frequency of high-arm grooming and %PPC (both sexes: r = −.101, n = 18, p = 0.69; males only: r = −0.114, n = 13, p = 0.71). Second, the periods during which dyads remained in a given high-arm grooming posture varied from 3 to 155 s (overall mean 46.7 s ± 27.4 s, n = 249 episodes). For adult males whose duration of high-arm grooming was recorded at least 20 times, we found no relationship between duration of high-arm grooming and the frequency of engaging in PPC (r = −.24, n = 7, p ns). Thus, neither of our potential indices of motivational interest in high-arm grooming showed any relationship to %PPC.

With regard to social factors, %PPC did not differ between dyads in which the partner was a close matrilineal kin (mother, offspring, or sibling) and those that were unrelated (%PPC in kin dyads 37.3% ± 34.8%, n = 12; non-kin dyads 31.2% ± 24.3%, n = 13; dyads with at least ten photographs, Mann-Whitney z = 0.027, p ns). We also attempted to test whether %PPC was related to affiliative relationships between partners. We assessed the influence of strength of social relationship among 12 adult males by comparing %PPC with a combined association index (CAI). The CAI measured a dyad's deviation from the mean value across three independent indices of association, i.e., time spent in the same party, the frequency of the two individuals being within 5 m of each other when they were in the same party, and the frequency of being nearest neighbors, given that they were within 5 m of each other [12]. For the 13 male-male dyads with at least ten photographed episodes, there was no hint of a positive correlation between %PPC and CAI (r = −0.31, n = 13).

Previous research has shown that young chimpanzees learn how to use feeding tools partly from their mothers, leading to similarities in tool-using behavior [3]. Similarly, there is evidence for maternal influence on the ontogeny of high-arm grooming. Thus, in Mahale, mothers tend to initiate such grooming with their offspring, remain their only high-arm grooming partner for up to 7 years, and have been seen to mold their young's high-arm posture [9]. We therefore examined maternal influences on %PPC. We found that mothers accounted for more than 80% of an offspring's high-arm grooming until the offspring reached 12 years old, i.e., early adulthood. To test the strength of maternal influences, we compared the PPC prevalence exhibited by all available adults or adolescents (those at least 10 years old, with at least ten photographs of high-arm grooming, where matrilineal kinship was known). Figure 3 shows that individual differences in %PPC were closely related to matrilineal relationships (intra-class correlation = 0.47; 95% CI: 0.17, 0.84; p < 0.0001). For example % PPC scores for three individuals in one matriline were all below 11%, while in another they were all above 50%. In two cases, the matriarch had died several years

Table 1. Frequency of PPC by Matriline

Matriline	# Individuals	%PPC Groom within Matriline: Mean ± Standard Deviation	%PPC Groom between Matriline: Mean ± Standard Deviation
OU	3	8.9 ± 4.2	10.0 ± 6.6
PU	2	9.1 ± 0.0	20.3 ± 2.7
TG	3	46.0 ± 22.0	30.4 ± 9.0
AL	3	59.6 ± 5.4	40.2 ± 20.9
LP	3	91.6 ± 1.1	38.9 ± 6.3

"# Individuals" shows number of individuals within the matriline: all individuals had at least ten data points for each cell. "%PPC Groom within Matriline" and "%PPC Groom between Matriline" show mean and standard deviations of %PPC of the members of each matriline. Matriline membership is shown in Figure 1.

earlier (deaths: PU in 2003, LP in 2004), but in each case, the remaining adult offspring resembled each other closely in their % PPC tendency (Figure 3).

Family differences in PPC tendencies were particularly pronounced when individuals groomed within matrilines. When chimpanzees high-arm groomed with mothers, offspring, or siblings, mean %PPC within matrilines varied over an order of magnitude, from 8.9% ± 4.2% (the OU family) to 91.6% ± 1.1% (the LP family) (Kruskal-Wallis $K = 11.9$, $df = 4$, $p < 0.02$) (Table 1). Even when grooming with individuals from other matrilines, which would often require at least one member of the dyad to adjust his/her grooming style, differences among family tendencies remained. For example, comparing episodes when they groomed outside their matrilines, the five members of the two matrilines showing the lowest %PPC (OU, PU) all engaged less frequently in PPC than any of the six members of the two matrilines showing the highest %PPC (AL, LP) (Table 1).

An intriguing question concerns the probability of PPC when individuals from high-%PPC and low-%PPC families groomed with each other, since this context required one of the individuals to abandon its usual style. A predictable tendency for a class of individuals (such as low-%PPC individuals, or those who have a low dominance rank) to adopt the style of their partner in these circumstances would suggest a mechanism by which horizontal transmission of grooming style could occur. For instance, the mechanism could be a rule such as "if your partner is dominant, allow him or her to initiate and then accept their grooming style."

We identified high-%PPC individuals as those with the top ten %PPC scores regardless of who their partner was (n = 3 females, 7 males; %PPC score range 35.7%–62.0%). To find individuals who tended to have a frequent form of high-arm grooming contact other than PPC, we classified all contacts as palm-to-palm, palm-to-wrist, palm-to-forearm, wrist-to-wrist (WW), wrist-to-forearm, forearm-to-forearm, or another combination (e.g., involving the fingers or the back of the hand) (Table S2). The second most frequent form was WW, defined as wrists providing the main contact for both partners. We identified high-%WW individuals as those with the top ten %WW scores (n = 1 female, 9 males; %WW score range 18.6%–41.4%).

For 14 dyads with at least 10 high-arm grooming episodes involving one high-%PPC partner (>60% PPC) and one high-% WW partner (>35% wrist-wrist contact), the dyad sometimes used PPC and sometimes did not. The sample size was small, but no overall pattern was noted, and age, sex, and social dominance played no detectable influence. For example, out of nine dyads in which one partner "won" more often (in the sense that the pair adopted that partner's most frequent type of contact), the older partner "won" in four cases and "lost" in five cases. Thus, currently we have no evidence of any horizontal transmission biases.

In high-arm grooming, the angles of the wrist and elbow can vary between bouts [1]. In most cases of PPC (64.2%), the elevated arms of both partners were straight, i.e., the angle of the elbow was judged to be 150°–180° (Figure 1). This raised the possibility that individual or family preference for the PPC contact was associated with, and could be due to, a preference for keeping an arm straight. However, we found no indication that matrilines varied in their tendency to groom with straight as opposed to flexed arms. For individuals with >40 photographs, the median percentage of high-arm grooming with two straight arms was 45.3%, and within every matriline, at least one member was above, and one below, the median. Variation among individuals in %PPC was therefore due to variation in the preference for PPC more than for holding arms straight.

The high consistency of %PPC within matrilines (Figure 3; Table 1) indicates relatively faithful transmission. Current evidence indicates a role for social learning, but genetic influences are also plausible since they have not been ruled out for behavioral variants among chimpanzee communities even where some degree of social learning is known to occur [13, 14]. Comparison with patrilineal relationships will eventually afford a test of genetic influences.

Why matrilines varied is unknown. Ultimately, we assume that differences come from non-faithful transmission, i.e., a daughter adopting a style other than her mother's. Possible sources of such "cultural mutation" could include injuries to a mother that constrain the nature of her hand or arm contact, or a female orphan adopting the PPC style of non-kin. Alternatively, in theory, some individuals might develop strong personal preferences that lead them to reject their mother's style.

Shifts in average PPC tendency within a community are expected from various demographic events. Mothers with many daughters who breed in their natal community, as can occur in Gombe, Tanzania [15], will disproportionately transmit their style over at least two generations. In contrast, mothers who have only sons, or whose daughters all breed in other communities (as happens routinely in chimpanzees [16]), will have an impact over one generation only. Changes in the group average are therefore expected across generations.

Chimpanzees have sometimes been suggested to change their behavioral styles so as "to aid social cohesion and the maintenance of group dynamics" [17–19] (quote is from pg. 1200 in [17]). In support of that idea, in two cases (nut-smashing, ant-dipping), neighboring communities of wild chimpanzees have been shown to use tools in different ways for solving what appeared to be ecologically identical problems [20, 21]. If PPC signals social affiliation, however, our evidence suggests that it does so only at the level of the matrilineal family.

Results support the role of individual conservatism as an explanation for the frequency distribution of PPC, and they

provide the first observational data from the wild in support of experiments showing that when incentives are low, chimpanzees tend to maintain their first-learned strategy rather than conform to the group [22]. Individuals learning a novel technique of tool use in captivity showed a similar tendency [23]. Whether the same mechanism accounts for the distribution of PPC elsewhere in the wild is unknown. In the Chimfunshi sanctuary, where community members have no long-term matrilineal lineages, %PPC reaches more than 80% [2]. This suggests that other mechanisms are possible. The importance of matrilineal inheritance for cultural traditions in general is therefore an interesting open question.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.09.005.

AUTHOR CONTRIBUTIONS

Conceptualization, R.W.W.; Validation, K.K. and J.R.; Investigation, R.W.W., Z.P.M., and S.W.; Resources, R.W.W., A.B.B., N.F.B., R.D., C.W., and E.O.; Data Curation, Z.P.M.; Writing – Original Draft, R.W.W.; Writing – Review & Editing, R.W.W., K.K., Z.P.M., and M.N.M.; Funding Acquisition, R.W.W., Z.P.M., and M.N.M.; Supervision, R.W.W and M.N.M.

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REFERENCES

1. Nakamura, M., and Uehara, S. (2004). Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social customs. Curr. Anthropol. *45*, 108–114.
2. van Leeuwen, E.J.C., Cronin, K.A., Haun, D.B.M., Mundry, R., and Bodamer, M.D. (2012). Neighbouring chimpanzee communities show different preferences in social grooming behaviour. Proc. Biol. Sci. *279*, 4362–4367.
3. Lonsdorf, E.V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (Pan troglodytes schweinfurthii)? Anim. Cogn. *9*, 36–46.
4. Rendell, L., and Whitehead, H. (2001). Culture in whales and dolphins. Behav. Brain Sci. *24*, 309–324, discussion 324–382.
5. Cantor, M., and Whitehead, H. (2013). The interplay between social networks and culture: theoretically and among whales and dolphins. Philos. Trans. R. Soc. Lond. B Biol. Sci. *368*, 20120340.
6. McGrew, W.C., and Tutin, C.E.G. (1978). Evidence for a social custom in wild chimpanzees? Man (Lond) *13*, 234–251.
7. Webster, T.H., Hodson, P.R., and Hunt, K.D. (2009). Grooming hand-clasp by chimpanzees of the Mugiri community, Toro-Semliki Wildlife Reserve, Uganda. Pan African News *16*, 5–7.
8. de Waal, F.B.M., and Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. Am. J. Primatol. *43*, 339–346.
9. Nakamura, M., and Nishida, T. (2013). Ontogeny of a social custom in wild chimpanzees: age changes in grooming hand-clasp at Mahale. Am. J. Primatol. *75*, 186–196.
10. McGrew, W.C., Marchant, L.F., Scott, S.E., and Tutin, C.E.G. (2001). Intergroup differences in a social custom of wild chimpanzees: the grooming hand-clasp of the Mahale Mountains. Curr. Anthropol. *42*, 148–153.
11. van Leeuwen, E.J.C., Kendal, R.L., Tennie, C., and Haun, D.B.M. (2015). Conformity and its look-a-likes. Anim. Behav. *110*, e1–e4.
12. Gilby, I.C., and Wrangham, R.W. (2008). Association patterns among wild chimpanzees (Pan troglodytes schweinfurthii) reflect sex differences in cooperation. Behav. Ecol. Sociobiol. *62*, 1831–1842.
13. Langergraber, K., Schubert, G., Rowney, C., Wrangham, R., Zommers, Z., and Vigilant, L. (2011). Genetic differentiation and the evolution of cooperation in chimpanzees and humans. Proc. Biol. Sci. *278*, 2546–2552.
14. Corbey, R., Jagich, A., Vaesen, K., and Collard, M. (2016). The Acheulean handaxe: More like a bird's song than a beatles' tune? Evol. Anthropol. *25*, 6–19.
15. Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior (Harvard University Press).
16. Stumpf, R.M., Emery Thompson, M., Muller, M.N., and Wrangham, R.W. (2009). The context of female dispersal in Kanyawara chimpanzees. Behaviour *146*, 629–656.
17. Hopper, L.M., Schapiro, S.J., Lambeth, S.P., and Brosnan, S.F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. Anim. Behav. *81*, 1195–1202.
18. van Schaik, C.P. (2012). Animal culture: chimpanzee conformity? Curr. Biol. *22*, R402–R404.
19. de Waal, F.B.M. (2001). The Ape and the Sushi-Master: Cultural Reflections of a Primatologist (Harvard University Press).
20. Luncz, L.V., and Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. Am. J. Primatol. *76*, 649–657.
21. Koops, K., Schöning, C., Isaji, M., and Hashimoto, C. (2015). Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. Sci. Rep. *5*, 12456.
22. Van Leeuwen, E.J.C., Cronin, K.A., Schütte, S., Call, J., and Haun, D.B.M. (2013). Chimpanzees (Pan troglodytes) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. PLoS ONE *8*, e80945.
23. Whiten, A., Horner, V., and de Waal, F.B.M. (2005). Conformity to cultural norms of tool use in chimpanzees. Nature *437*, 737–740.