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**Distribution of a chimpanzee social custom is explained by matrilineal relationship rather than conformity.**

Richard W. Wrangham<sup>1</sup>, Kathelijne Koops<sup>1,2</sup>, Zarin P. Machanda<sup>1,3</sup>, Steven Worthington<sup>4</sup>, Andrew B. Bernard<sup>5</sup>, Nicholas F. Brazeau<sup>6</sup>, Ronan Donovan<sup>7</sup>, Jeremiah Rosen<sup>1</sup>, Claudia Wilke<sup>8</sup>, Emily Otafi<sup>9</sup>, Martin N. Muller<sup>10</sup>

<sup>1</sup> Harvard University, Department of Human Evolutionary Biology, 11 Divinity Avenue, Cambridge, MA 02138, USA

<sup>2</sup> University of Zurich, Anthropological Institute and Museum, Winterthurerstrasse 190, 8057 Zürich, Switzerland

<sup>3</sup> Tufts University, Department of Anthropology, 5 The Green, Medford, MA 02155, USA

<sup>4</sup> Harvard University, Institute for Quantitative Social Science, 1737 Cambridge Street, Cambridge, MA 02138, USA

<sup>5</sup> University of Michigan, Department of Anthropology, 101 West Hall, S. University Avenue, Ann Arbor, MI 48109, USA

<sup>6</sup> University of North Carolina, Department of Epidemiology, Gillings School of Global Public Health, 1335 Dauer Drive, Chapel Hill, NC 27599, USA

<sup>7</sup> National Geographic Magazine, 1144 17<sup>th</sup> Street NW, Washington DC 20036, USA

<sup>8</sup> University of York, Department of Psychology, James Way, Heslington, York YO10 5DD, UK

<sup>9</sup> Makerere University Biological Field Station, Kibale Chimpanzee Project, Kamwenge Road, Fort Portal, Uganda

<sup>10</sup> University of New Mexico, Department of Anthropology, Albuquerque, NM 87131,  
USA

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Correspondence to: Richard Wrangham (email: [wrangham@fas.harvard.edu](mailto:wrangham@fas.harvard.edu))

## 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 matriline, 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-using 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 longterm 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 (Fig. 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 holds 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 three of eleven wild populations high-arm grooming is absent, suggesting that elsewhere it is socially learned [7] (see SI). In support of social learning, the western and eastern subspecies 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 (Fig. 1a) [10]; and %PPC is the proportion of an individual's high-arm grooming bouts featuring palm-to-palm-clasping. Our aim is to

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. 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  $\pm$  standard deviation =  $76.5 \pm 28.6$  per individual, range 42-128). Across individuals %PPC ranged from 6.8% to 57.8% (mean  $\pm$  standard deviation  $32.6\% \pm 18.9\%$ ).

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% (Fig. 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 Fig. 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 onwards) and difference between an individual's %PPC score and the group median (Pearson  $r = 0.14$ ,  $n = 18$ ,  $p$  ns). In sum we found no evidence that individuals converged in their frequencies of palm-to-palm-clasping.

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  $44.9\% \pm 25.9\%$ ,  $n = 16$ ; males  $48.8\% \pm 17.9\%$ ,  $n = 16$ ; Mann-Whitney  $U = 89.5$ ,  $z = 0.93$ ,  $P$  n.s.; Table S1). Thus the sex difference in time spent in 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  $32.0\% \pm 17.3\%$ ,  $n = 13$ ; female  $34.1\% \pm 24.7\%$ ,  $n = 5$  Mann-Whitney  $U = 31$ ,  $z = 0.099$ ,  $P = .92$ ; Table S2). There was also no relationship between %PPC and age ( $r = .03$ ,  $n = 18$ ,  $P$  ns, range 9 – ~58 years; Table S2). Thus %PPC was not related to either sex or age.

A higher tendency for palm-to-palm-clasping 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

hours 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 seconds (overall mean  $46.7 \text{ s} \pm 27.4 \text{ s}$ ,  $n = 249$  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  $37.3\% \pm 34.8\%$ ,  $n = 12$ ; non-kin dyads  $31.2\% \pm 24.3\%$ ,  $n = 13$ ; dyads with at least 10 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 meters of each other when they were in the same party, and the frequency of being nearest neighbors, given that they were within 5 meters of each other [12]. For the 13 male-male dyads with at least 10 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 ten years old, with at least 10 photographs of high-arm grooming, where matrilineal kinship was known). Fig. 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 earlier (deaths: PU in 2003, LP in 2004), but in each case the remaining adult offspring resembled each other closely in their %PPC tendency (Fig. 3).

Family differences in PPC tendencies were particularly pronounced when individuals groomed within matrilineal lines. When chimpanzees high-arm groomed with mothers, offspring or siblings, mean %PPC within matrilineal lines varied over an order of magnitude, from  $8.9\% \pm 4.2\%$  (the OU family) to  $91.6\% \pm 1.1\%$  (the LP family) (Kruskal-Wallis  $K = 11.9$ ,  $df = 4$ ,  $P < 0.02$ ) (Table 1). Even when grooming with individuals from other matrilineal lines, 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 matriline, the five members of the two matriline showing the lowest %PPC (OU, PU) all engaged less frequently in PPC than any of the six members of the two matriline showing the highest %PPC (AL, LP) (Table 1).

An intriguing question concerns the probability of palm-to-palm-clasping 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, wrist-to-forearm, forearm-to-forearm, or another combination (e.g. involving the fingers or the back of the hand) (SI, Table 2). The second most frequent form was wrist-to-wrist (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 9 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 palm-to-palm-clasping (64.2%) the elevated arms of both partners were straight, i.e. the angle of the elbow was judged to be  $150^{\circ}$  -  $180^{\circ}$  (Fig. 1). This raised the possibility that individual or family preference for the palm-to-palm-clasp contact was associated with, and could be due to, a preference for keeping an arm straight. However, we found no indication that matriline 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 palm-to-palm-clasping more than for holding arms straight.

The high consistency of %PPC within matriline (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 matrilineal 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 p. 1200 in ref. 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 palm-to-palm-clasping 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 palm-to-palm-clasping, 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 longterm 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.

## **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.M., M.N.M.; Supervision, R.W.W. and M.N.M.

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## Figure Legends

### **Figure 1. Styles of high-arm grooming.**

(a) Palm-to-palm-clasp (photo: Suzi Eszterhas). (b) Forearm-to-forearm contact (photo: Andrew Bernard). Types of contact of upper arms include diverse combinations of hand, wrist and arm. Arms can be straight or bent. Fig. 1(b) illustrates why the term ‘high-arm grooming’ is more appropriate than ‘hand-clasp grooming’.

### **Figure 2. Individual differences in frequency of palm-to-palm-clasping within the Kanyawara community.**

%PPC = percentage of high-arm grooming episodes in which the individual exhibited palm-to-palm-clasping. 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 in Fig. 2 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. Palm-to-palm-clasping frequency by matriline.**

Y-axis shows %PPC (palm-to-palm-clasp) 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 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.

Table 1. Frequency of palm-to-palm-clasping (PPC) by matriline.

Matriline	# individuals	% PPC groom	% PPC groom
		<i>within</i> matriline	<i>between</i> matriline
		Mean $\pm$ StDev	Mean $\pm$ StDev
OU	3	8.9 $\pm$ 4.2	10.0 $\pm$ 6.6
PU	2	9.1 $\pm$ 0.0	20.3 $\pm$ 2.7
TG	3	46.0 $\pm$ 22.0	30.4 $\pm$ 9.0
AL	3	59.6 $\pm$ 5.4	40.2 $\pm$ 20.9
LP	3	91.6 $\pm$ 1.1	38.9 $\pm$ 6.3

“# individuals” shows number of individuals within the matriline: all individuals had at least 10 data-points for each cell. % PPC groom: mean and standard deviations of %PPC of the members of each matriline. Matriline membership is shown in Fig. 1.