

a percept that is elicited by cone activation. This indicates a failure of lightness constancy at low light levels. Even though something appears white during photopic viewing, it does not appear white at scotopic luminance levels, and even white cats at night appear gray.

SUPPLEMENTAL INFORMATION

Supplemental Information includes a description of the experimental methods and two figures, as well as further details on the experiment that used the smaller paper chips and the experiment that used a monitor to produce self-luminous patches, and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.05.008>.

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Chimpanzee culture extends beyond matrilineal family units

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The ‘grooming handclasp’ is one of the most well-established cultural traditions in chimpanzees. A recent study by Wrangham *et al.* [1] reduced the cultural scope of grooming-handclasp behavior by showing that grooming-handclasp style convergence is “explained by matrilineal relationship rather than conformity” [1]. Given that we previously reported cultural differences in grooming-handclasp style preferences in captive chimpanzees [2], we tested the alternative view posed by Wrangham *et al.* [1] in the chimpanzee populations that our original results were based on. Using the same outcome variable as Wrangham *et al.* [1] — the proportion of high-arm grooming featuring palm-to-palm clasping — we found that matrilineal relationships explained neither within-group homogeneity nor between-group heterogeneity, thereby corroborating our original conclusion that grooming-handclasp behavior can represent a group-level cultural tradition in chimpanzees.

Wrangham *et al.* [1] investigated how and why individuals differed in their tendency to engage in palm-to-palm clasping, and whether any variation could be explained by demographic (for example, sex or age) and/or individual (for example, motivation) factors in the chimpanzees of the Kanyawara community, looking at 35 individuals and 932 bouts of grooming handclasps. The authors concluded that “chimpanzees conform in their grooming styles only to their mothers, not to the larger group” [1]. Importantly, the authors keep open the option that other mechanisms might be guiding grooming-handclasp behavior by referring to the fact that chimpanzees at the Chimfunshi Wildlife Orphanage

Trust, Zambia, seemed to reach high frequencies of palm-to-palm clasping in the absence of long-term matrilineal relationships [1].

The Chimfunshi chimpanzees not only exhibited high palm-to-palm clasping frequencies, but their handclasp-style preferences matched within and differed between groups [2]. In contrast to the assumption made by Wrangham *et al.* [1], the handclasping groups at Chimfunshi house 16 family units (versus 5 at Kanyawara [1]), up to the third generation. Crucially, this fact allowed us to validate the claim by Wrangham *et al.* [1] that chimpanzee culture is limited to convergence within matrilineal family units or, in contrast, potentially demonstrate group-level culture in chimpanzees. To test this, we incorporated matrilineal relationships into our original models and applied these models to the largest data set on grooming-handclasp styles in chimpanzees to date. See the Supplemental Information for details on experimental procedures and statistical analyses.

Using data from two different groups across three years and including only those chimpanzees with known matrilineal relationships (42 individuals from 16 matrilineal relationships), we found that matrilineal relationship did not obviously contribute to variation in palm-to-palm clasping frequency in the Chimfunshi chimpanzees (1,033 bouts of grooming handclasps recorded; permutations of matriline within a generalized linear mixed model context, $\chi^2=3.22$, $p=0.44$, and estimated standard deviations for random intercept and random slopes of matrilineal relationships (SDs): all <0.5). Focusing on within-group tendencies, we again found no obvious effect of matrilineal relationships on chimpanzees’ tendency to engage in palm-to-palm clasping (for group 1, featuring 12 individuals, 4 matrilineal relationships and 230 bouts of grooming handclasps, $\chi^2=5.07$, $p=0.44$ and SDs <1; for group 2, featuring 30 individuals, 12 matrilineal relationships and 803 bouts of grooming handclasps, $\chi^2=2.91$, $p=0.43$ and SDs <0.7). Importantly, our originally reported group differences in palm-to-palm clasping [2] were confirmed while controlling for the effect of matrilineal relationships ($\chi^2=6.33$, $df=1$, $p=0.014$; Figure 1).

We analyzed our data with an appropriate random-effect structure

(that is, including random slopes when variation allows) in order to prevent Type I errors [3–5]. Nonetheless, to preclude potentially unwarranted dismissal of matrilineal effects on palm-to-palm clasping, and based on arguments against using an almost maximal random-effects structure ([6] referring to [7]), we additionally fitted two more series of models with an increasingly minimal random-effects structure. The first series comprised our primary model excluding the random slope terms within matriline (thus, for matriline, only leaving the random intercept). We found that matrilineal relationships affected palm-to-palm clasping tendencies neither across groups ($\chi^2=2.52$, $p=0.40$; SDs < 0.5) nor within groups (group 1, $\chi^2=2.52$, $p=0.41$, and SDs < 1; group 2, $\chi^2=2.52$, $p=0.35$ and SDs < 0.3), hence corroborating our primary results. The second series comprised our fixed-effects model including only the random intercepts of subject, dyad, matriline identity, date and bout number. Again, matrilineal relationships affected palm-to-palm clasping tendencies neither across groups ($\chi^2=2.86$, $p=0.41$, and SDs < 0.5) nor within groups (group 1, $\chi^2=6.96$, $p=0.43$ and SDs < 1; group 2, $\chi^2=0.94$, $p=0.30$ and SDs < 0.3). Note that all these results point in the same direction: contrary to what was observed in the Kanyawara chimpanzees [1], the tendency to engage in palm-to-palm clasping cannot be sufficiently explained by matrilineal relationships in the Chimfunshi chimpanzees.

To reiterate, Wrangham *et al.* [1] recently reported that chimpanzees' grooming-handclasp-style preferences might be better explained by retention of matrilineal styles than group-level social learning mechanisms. Our results, however, suggest that at least in Chimfunshi, social learning in chimpanzees occurs beyond family units, thus creating the within-group homogeneity and between-group heterogeneity in trait expression, characteristic of cultural diversity [8]. Contemplating the discrepancy between findings, we suggest that a higher frequency of group fusions in the Chimfunshi compared to the Kanyawara populations may account for the extended social-learning tendencies in our study. The Chimfunshi chimpanzees are provided with supplementary provisions once a day, causing the

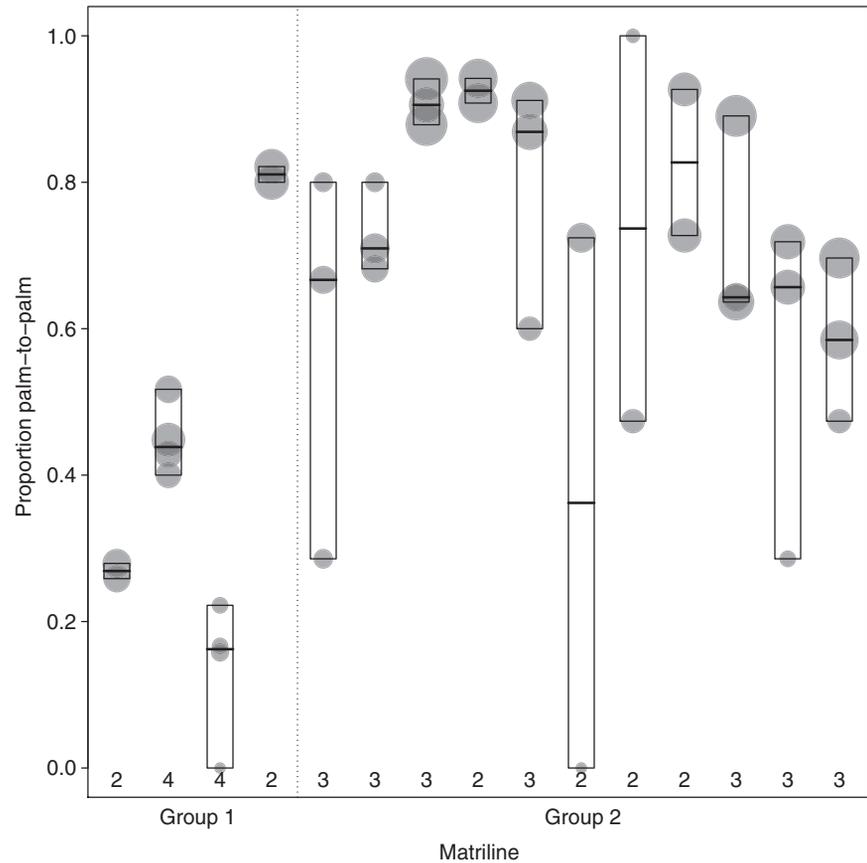


Figure 1. Chimpanzee handclasp grooming at the Chimfunshi Wildlife Orphanage Trust. Proportion of individuals' engagement in palm-to-palm handclasping (y-axis) for two isolated groups of chimpanzees (separated by vertical dotted line). Each box represents one matriline and the size of the matrilineal units is indicated above the x-axis. Medians of each matriline are represented by the solid, horizontal lines within the boxes, which represent the range in palm-to-palm clasping preference of each matriline. Circle area corresponds to the number of observations contributing to one individual's palm-to-palm clasping score.

entire group to emerge from the bush and congregate. In anticipation of the provisioning, chimpanzees engage in grooming-handclasp behavior relatively frequently (our unpublished data). In conjunction, these aspects may create conditions in which social learning may extend beyond family units. Alternatively, given the existing evidence for intraspecific variation in social tolerance across groups of chimpanzees [9], we hypothesize that differences in group cohesion between the Kanyawara and Chimfunshi communities may account for the respective discrepancy. This hypothesis is supported by the fact that group-level grooming-handclasp-style convergence at Chimfunshi was highest in the most socially tolerant group [2,9]. We concur with Wrangham *et al.* [1] in the conclusion that it remains an exciting endeavor to investigate the

underlying mechanism(s) guiding group-level convergence of socially acquired behavior in chimpanzees. Notably, this mechanism does not need to be 'conformity', but could be any (set of) mechanism(s) leading to within-group convergence and/or between-group divergence [10].

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures and supplemental references and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.05.003>.

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AUTHOR CONTRIBUTIONS

E.J.C.v.L. conceived the study. E.J.C.v.L. and R.M. developed the methodology. E.J.C.v.L. wrote the original draft, and E.J.C.v.L., K.A.C., R.M., M.B., and D.B.M.H. reviewed and edited the manuscript.

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Response to: Chimpanzee culture extends beyond matrilineal family units

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We thank van Leeuwen *et al.* [1] for their response to our finding that matrilineal relationships strongly influence the style of high-arm grooming in wild chimpanzees of the Kanyawara community. We agree with them that grooming styles could be transmitted by different mechanisms in different contexts, and we appreciate their effort to assess whether the transmission of grooming styles within two captive groups in Chimfunshi accords with our result.

The style in question is palm-to-palm clasp (also known as mutual palm-clasp, and sometimes as handclasp grooming). Palm-to-palm clasp occurs during high-arm grooming. Confusingly, high-arm grooming has traditionally been called ‘handclasp grooming’ even though it includes a variety of styles (such as wrist-to-wrist grooming) in addition to palm-to-palm clasp. van Leeuwen *et al.* [1] attributed to us the idea that we “questioned the validity of the grooming handclasp as cultural tradition”. In fact, however, we follow previous researchers in concluding that these behaviors are culturally transmitted. As we argued previously, the grooming style appears to be influenced by social learning at two levels. First, populations of chimpanzees vary in whether they practice high-arm grooming at all. Second, within social communities, individuals vary in how frequently their high-arm grooming involves palm-to-palm clasp and we found that individuals within the same matriline tended to show similar proportions of palm-to-palm clasp. The two levels raise complementary problems. The first concerns the question of why high-arm grooming is found in some populations

and not others. The second concerns the question of why the proportion of palm-to-palm clasp varies among high-arm groomers. Given the reported evidence for social learning, we regard both kinds of variation as cultural [2].

As we noted previously [2], in the Chimfunshi sanctuary, mechanisms other than matrilineal inheritance might be found to explain the distribution of palm-to-palm clasp frequencies. Van Leeuwen *et al.* [1] now suggest that this is the case. Unfortunately, they did not examine whether conformity occurred, for example, by assessing whether there was an average rate of palm-to-palm clasp within matrilines on which individuals tended to converge. Instead they claim that the distribution of palm-to-palm clasp frequency was not explained by matrilineal relationship. We are puzzled by their conclusion because their Figure 1 seems to show that at least in Group 1, individual values of palm-to-palm clasp frequency were clustered by matriline.

Van Leeuwen *et al.* [1] tested the null hypothesis that, on average, the probability of engaging in palm-to-palm clasp will not differ between grooming dyads consisting of individuals from the same matriline and dyads comprised of individuals from separate matrilines. They use generalized linear mixed models and likelihood ratio tests to determine the statistical significance of the matrilineal effect within and among two groups of chimpanzees, but do not report effect sizes. The likelihood ratio tests failed to reject the null hypothesis of no matrilineal effect, with p values of $p=0.28$ for Group 1, $p=0.99$ for Group 2, and $p=1$ for the combined groups. We urge caution, however, in the interpretation of these results. Failure to reject a null hypothesis in no way demonstrates support for that null hypothesis. A p value greater than 0.05 indicates that the 95% confidence interval for the matriline effect encompasses zero (that is, no effect), but this does not preclude the confidence interval from encompassing many other, potentially large effect sizes. This is because the confidence interval consists of a range of plausible effect sizes that cannot be rejected. It is possible, therefore, that the Chimfunshi chimpanzees’ frequency of palm-to-palm-clasp behavior is explained