

1 **Chimpanzee Culture Extends Beyond Matrilineal Family Units**

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

31         Given that previous studies have shown that chimpanzees learn skills from their  
32 mothers [2-4], Wrangham et al. [1] investigated whether the most common style of GHC  
33 behavior – PPC – followed a pattern based on demographic (e.g., sex, age) and/or individual  
34 (e.g., motivation to engage in GHC) factors in the chimpanzees of the Kanyawara community  
35 of Kibale National Park, western Uganda ( $n_{\text{individuals}}=35$ ;  $n_{\text{GHC bouts}}=932$ ). Their main goal was  
36 to understand how and why individuals differed in their tendency to engage in PPC [1]. By  
37 means of a series of independent statistical tests, Wrangham et al. [1] concluded that only  
38 matrilineal relationships significantly influenced individuals’ PPC tendencies. In turn, the  
39 conclusion was advanced that “chimpanzees conform in their grooming styles only to their  
40 mothers, not to the larger group” [1]. Importantly, Wrangham et al. [1] keep open the option  
41 that other mechanisms might be at play in chimpanzees’ GHC behavior by referring to the  
42 fact that chimpanzees at the Chimfunshi Wildlife Orphanage Trust, Zambia, seemed to reach  
43 high frequencies of PPC in the absence of long-term matrilineal relationships [1].

44         The Chimfunshi chimpanzees have been reported to not only exhibit high frequencies  
45 of PPC, but, notably, their GHC-style tendencies matched within groups and differed between  
46 groups [2]. Based on this group-level variation in GHC style – which cannot be accounted for

47 by genetic or ecological differences across groups – van Leeuwen et al. concluded that  
48 “chimpanzees’ social behavior is not only motivated by innate predispositions and individual  
49 inclinations but may also be partly cultural in nature” [2]. Moreover, in contrast to Wrangham  
50 et al. [1]’s assumption, Chimfunshi houses many family units (n=16) up to the third  
51 generation. Here, we aimed to test whether chimpanzees’ GHC-style may be restricted to  
52 social learning within matrilineal relationships [1] or whether chimpanzees’ social learning of  
53 GHC-style extends beyond family units by re-analyzing our original data in light of possible  
54 effects of matrilineal relationships. We chose to incorporate matrilineal relationships into our  
55 original models (instead of performing separate statistical tests [1]) in order to test multiple  
56 predictors simultaneously and control for repeated observations of individuals and dyads.

57 Crucially, using data from two different groups across three years, and including only  
58 those chimpanzees with known matrilineal relationships (cf. [2]), we found that matrilineal relationship did  
59 not obviously contribute to variation in PPC frequency in the Chimfunshi chimpanzees  
60 (permutations of matriline within GLMM context:  $\chi^2 = 3.22$ ,  $p = 0.44$ ; estimated standard  
61 deviations for random intercept and random slopes of matrilineal relationships: all  $< 0.5$ ;  $n_{\text{ind}} = 42$ ,  $n_{\text{matrilineal}} =$   
62  $16$ ,  $n_{\text{bouts}} = 1033$ ). Similar results were obtained when focusing on *within*-group tendencies,  
63 i.e., no obvious effect of matrilineal relationships on chimpanzees’ tendency to engage in PPC  
64 (group 1:  $\chi^2 = 5.07$ ,  $p = 0.44$ ;  $SDs < 1$ ;  $n_{\text{ind}} = 12$ ,  $n_{\text{matrilineal}} = 4$ ,  $n_{\text{bouts}} = 230$ ; group 2:  $\chi^2 = 2.91$ ,  $p =$   
65  $0.43$ ;  $SDs < 0.7$ ;  $n_{\text{ind}} = 30$ ,  $n_{\text{matrilineal}} = 12$ ,  $n_{\text{bouts}} = 803$ ). Importantly, our originally reported  
66 group differences in PPC [2] were confirmed while controlling for the effect of matrilineal  
67 relationships ( $\chi^2 = 6.33$ ,  $df = 1$ ,  $p = 0.014$ ; Figure 1).

68 Note that we analyzed our data with a random effect structure *sensu* the most  
69 established method to date (i.e., including random slopes when variation allows, in order to  
70 prevent Type I errors) [6-8]. Nonetheless, in order to preclude potentially unwarranted  
71 dismissal of matrilineal effects on PPC grooming, and based on arguments against using a  
72 (close to) maximal random effects structure ([9] referring to [10]), we additionally fitted two

73 more series of models with an increasingly minimal random effects structure. The first series  
74 comprised our primary model excluding the random slope terms within matriline (thus, for  
75 matriline, only leaving the random *intercept*). Matrilineal relationships neither obviously  
76 affected PPC tendencies *across* groups ( $\chi^2 = 2.52, p=0.40$ ; SDs < 0.5), nor *within* groups  
77 (group 1:  $\chi^2 = 2.52, p=0.41$ ; SDs < 1; group 2:  $\chi^2 = 2.52, p=0.35$ ; SDs < 0.3), hence  
78 corroborating our results. The second series comprised our fixed effects model including only  
79 the random *intercepts* of subject, dyad, matriline identity, date and bout number. Again,  
80 matrilineal relationships were neither obviously affecting PPC tendencies *across* groups ( $\chi^2 =$   
81  $2.86, p=0.41$ ; SDs < 0.5). nor *within* groups (group 1:  $\chi^2 = 6.96, p=0.43$ ; SDs < 1; group 2:  $\chi^2$   
82  $= 0.94, p=0.30$ ; SDs < 0.3). For more details, see Supplemental Information.

83 Note that all these results point into the same direction: contrary to the Kanyawara  
84 chimpanzees as reported by Wrangham et al. [1], the tendency to engage in PPC grooming  
85 cannot be sufficiently explained by matrilineal relationships in the Chimfunshi chimpanzees.

86

87 FIGURE 1.

88

89 Recapitulating, Wrangham et al. [1] recently reported that chimpanzees' GHC-style  
90 preferences might be better explained by retention of matrilineal styles than group-level social  
91 learning mechanisms. Our results, however, suggest that at least in captive populations,  
92 chimpanzees may spontaneously extend their social learning efforts beyond family units, thus  
93 creating the within-group homogeneity and between-group heterogeneity in trait expression  
94 characteristic of cultural diversity [11]. Contemplating the discrepancy between Wrangham et  
95 al. [1]'s findings and ours, we suggest that potentially a higher frequency of group fusions in  
96 the Chimfunshi compared to the Kanyawara populations may account for the extended social  
97 learning tendencies in our study. The Chimfunshi chimpanzees are supplementary  
98 provisioned once a day, causing the entire group to retreat from the bush and congregate in a

99 relatively small space. In anticipation of the provisioning, the chimpanzees typically engage  
100 in GHC behavior relatively frequently (unpublished data). In conjunction, these aspects may  
101 create the conditions in which social learning may readily extend beyond family units.  
102 Alternatively, given the existing evidence for intraspecific variation in social tolerance across  
103 groups of chimpanzees [12], we hypothesize that differences in group cohesion between the  
104 Kanyawara and Chimfunshi communities may account for the respective discrepancy. This  
105 hypothesis is supported by the fact that group-level GHC-style convergence at Chimfunshi  
106 was highest in the most socially tolerant group (cf. [2, 12]). We extend Wrangham et al. [1]’s  
107 conclusion that it remains an exciting endeavor to investigate the underlying mechanism(s)  
108 guiding group-level convergence of socially-acquired behavior in chimpanzees. Notably, this  
109 mechanism does not need to be “conformity” but could be any (set of) mechanism(s) leading  
110 to within-group convergence (see group 2, also in [2]) and/or between-group divergence [13].  
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149

150 **Figure legends**

151

152 **Figure 1.** Proportion of individuals' engagement in palm-to-palm handclasping (*y*-axis) for  
153 two isolated groups of chimpanzees (separated by vertical dotted line). Each box represents  
154 one matriline and the size of the matrilineal units is indicated above the *x*-axis. Medians of  
155 each matriline are represented by the solid, horizontal lines within the boxes, which represent  
156 the range in PPC preference of each matriline. Circle area corresponds to the number of  
157 observations contributing to one individual's PPC score.

158

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160

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171

172 **In brief**

173

174 The style of high-arm grooming, or “grooming handclasp”, in the Kanyawara chimpanzees  
175 has recently been shown to be consistent within matrilineal family units, but not beyond. Van  
176 Leeuwen et al. show that in other populations, style homogeneity extends beyond families,  
177 thus revealing chimpanzee handclasping to be a group-level cultural phenomenon.