

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: χ^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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150 **Figure legends**

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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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166

167 **Author contributions**

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171

172 **In brief**

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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.