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Neighbouring chimpanzee communities show different preferences in social grooming behaviour

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Grooming handclasp (GHC) behaviour was originally advocated as the first evidence of social culture in chimpanzees owing to the finding that some populations engaged in the behaviour and others do not. To date, however, the validity of this claim and the extent to which this social behaviour varies between groups is unclear. Here, we measured (i) *variation*, (ii) *durability* and (iii) *expansion* of the GHC behaviour in four chimpanzee communities that do not systematically differ in their genetic backgrounds and live in similar ecological environments. Ninety chimpanzees were studied for a total of 1029 h; 1394 GHC bouts were observed between 2010 and 2012. Critically, GHC style (defined by points of bodily contact) could be systematically linked to the chimpanzee's group identity, showed temporal consistency both within and between groups, and could not be accounted for by the arm-length differential between partners. GHC has been part of the behavioural repertoire of the chimpanzees under study for more than 9 years (surpassing *durability* criterion) and spread across generations (surpassing *expansion* criterion). These results strongly indicate that chimpanzees' social behaviour is not only motivated by innate predispositions and individual inclinations, but may also be partly cultural in nature.

Keywords: group differences; *Pan troglodytes*; grooming handclasp; traditions; Chimfunshi Wildlife Orphanage Trust; social culture

1. INTRODUCTION

Grooming handclasp (GHC) behaviour was the first social behaviour to be described as a 'social custom' in chimpanzees [1]. This claim was based on the observation that the chimpanzees of the K(ajabala)-group in the Tanzanian Mahale mountains engaged in a peculiar social behaviour in which two individuals extend one arm overhead and clasp each other's upraised hands while grooming each other with the other arm, while the well-studied chimpanzees of the nearby Gombe field site were never observed engaging in it [1]. In their influential paper, McGrew & Tutin elaborate on the importance of this finding by arguing that this present/absent distinction cannot be explained by genetic predispositions nor by environmental factors. This line of reasoning led the authors to conclude that the GHC behaviour contains the necessary prerequisites for it to be considered 'cultural' [1].

While McGrew & Tutin's arguments have been adopted by later researchers investigating GHC behaviour in chimpanzees [2–5], the core question of whether this particular social behaviour can be validly considered 'cultural' has escaped closer empirical scrutiny. We support

the view that a detailed look at the behavioural differences between groups beyond a mere present/absent distinction is necessary to reveal a species' capacity and tendency to adopt a group-specific behavioural variant [3,6–7]. This may be especially relevant in the case of GHC behaviour, with its current prevalence and similarity to innate predispositions: (i) since the late 1970s, GHC behaviour has been observed in at least 16 independent populations to date [8], and (ii) GHC behaviour closely resembles chimpanzees' natural tendency to mutually groom with arms clasped onto overarching branches and initiate grooming bouts with upraised arms [1,9]. Since these two observations seem to point more towards a genetic and/or ecological explanation, it seems essential to investigate further whether there are any systematic differences in the GHC behaviour between groups above and beyond those that can be accounted for by ecological and genetic factors. The crucial focus of the investigation would thus be the different execution of this social behaviour, not only whether some populations have added to their repertoire the clasping of hands, while others have not. Accordingly, here, we scrutinized *variation* in GHC style between four communities of chimpanzees that have not been part of the handclasp literature yet and provide the largest dataset of handclasp bouts analysed to date. Additionally, we applied four more criteria to assess whether GHC behaviour could be considered cultural

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Table 1. Demographic details of the four chimpanzee groups at the CWOT at the start of the study (May 2010), and the number of individuals that engaged in the GHC behaviour throughout the observation window of this study.

	group 1	group 2	group 3	group 4
years of formation	1984–1989	1990–1994	1995–1999	2000–2002
males	11	11	6	8
females	12	29	8	5
mean age (years)	16	14	13	12
age range (years)	2–29	2–33	0–25	2–19
no. of GHC individuals 2010	18	30	0	0
no. of GHC individuals 2011	15	33	4	0

in a conservative sense [6,10]: *durability* (lasting for at least six months), *expansion* (increasing number of performers over time), and the exclusion of *genetic* and *environmental* determinants.

To our knowledge, the studies by McGrew *et al.* [11] and Nakamura & Uehara [3] are the only investigations that systematically assessed the variance in GHC styles beyond the present/absent distinction. Building on the work of McGrew *et al.* [11], Nakamura & Uehara [3] investigated whether particular GHC styles could be reliably associated with either of the two communities under study: the K(ajabala)-group and the M(imekire)-group in the Mahale mountains, Tanzania. After analysing individual and group preferences based on ‘palm-contact’ and the angles in which both the wrist and the elbow of the clasping arm were flexed, they provisionally concluded that ‘palm-to-palm’ contact and the straight wrist during GHC bouts were signatures of the K-group, while the M-group used ‘palm-to-palm’ contact only very infrequently and was better characterized by the use of flexed wrists during hand-clasp grooming [3]. While these studies provided preliminary evidence that GHC behaviour might be (partly) cultural in nature, the conclusions were based on occurrences rather than individuals and a relatively limited sample size [3,11].

The aim of this study was to evaluate the amount of group-level variation that characterizes GHC behaviour in chimpanzees, using a large number of observations and testing whether the behaviour is durable, expanding and varies between groups independent of genetic and environmental determinants [6,10]. In pursuit of this aim, we first systematically observed all study groups to establish an initial GHC present/absent distinction. Second, we analysed whether there were any differences in the GHC styles between the groups that engaged in the GHC behaviour, and assessed whether the variation was consistent over time. Third, we determined when the GHC entered the behavioural repertoires of the groups under study, and investigated whether formerly naive individuals started handclasping by comparing the active dyads between 2007, 2010 and 2011. Finally, to investigate whether GHC styles were systematically influenced by physical properties, we measured the arm-length differential between GHC partners. Because chimpanzees typically engage in GHC behaviour with stretched arms, variation in arm length could possibly generate variation in the GHC style that is defined by the points of arm-contact (see §2). Importantly, we studied four semi-wild groups of chimpanzees that are socially isolated from one another, yet live in the same forest at the Chimfunshi Wildlife Orphanage Trust (CWOT) in Zambia. The individuals at CWOT that were born in the wild were probably taken

from their wild social group while infants, as is the case for most rescued sanctuary chimpanzees. Given that the youngest age at which GHC has been observed is 5 years and 9 months [4], it is a safe assumption that these individuals had no experience engaging in GHC behaviour prior to their arrival at CWOT, thus minimizing the potential carry-over effects of early experiences in the wild. Moreover, since CWOT accepted chimpanzees from all over Africa and the groups were formed based on the dates of the chimpanzees’ arrivals, the chimpanzee communities under study do not differ systematically in their genetic backgrounds. In conjunction, these factors render any observed differences between groups unlikely to be due to genetic or ecological influences.

2. METHODS

(a) *Subjects and field-site*

Subjects comprised 90 chimpanzees in four stable social groups (see table 1 for group details on years of formation, sex distribution, age and number of GHC subjects). The chimpanzees live under semi-wild conditions at the CWOT, a sanctuary in the north-western part of Zambia. Approximately half the chimpanzees were wild-born, the other half were mother-reared at the CWOT. The enclosures consist of fenced miombo forest and range in size from 20 to 80 hectares. Chimpanzees stay outside overnight and only come indoors for feeding at 11.30–13.30. Except for a few metres along the fence line between groups 3 and 4, the chimpanzees in the different groups cannot see each other. Three chimpanzees that are currently housed separately in groups 1 and 2 shared group membership during the initial group formation process.

(b) *Data collection procedure*

Data were collected through all-occurrence sampling [12], in which subjects were identified individually. Observation sessions took place for 10 days between May and July 2010 and 10 days between May and July 2011, from 8.00 to 11.45. This time window was chosen because the chimpanzees tend to spend their time relatively close (binocular distance) to the indoor holding spaces prior to feeding, thus increasing observation opportunities. In 2010, these observations were completed for all four groups, yielding a total of 150 h (37.5 h per group). In 2011, this methodology was repeated for the two groups that were known to engage in the GHC behaviour, yielding a total of 75 h of observation (37.5 h per group). During the observation sessions, all visible GHC bouts were both live-coded and video-recorded from an observation deck on top of the indoor facilities by three observers who recorded the identity and handclasp style.

Table 2. Frequencies of GHC styles during observation sessions across groups and years (in bouts).

style	group 1		group 2	
	2010	2011	2010	2011
forearm–forearm	1	0	4	0
forearm–palm	2	3	2	6
forearm–wrist	0	3	4	5
other–other	11	1	6	1
other–palm	1	0	3	0
other–wrist	0	0	2	0
palm–palm	75	48	252	238
palm–wrist	15	14	29	19
wrist–wrist	19	22	12	13

Binoculars were used. If identity and style could not be determined from live observation or video, the event was counted for overall frequency but excluded from other analyses. Reliability between the lead observers of groups 1 and 2 was further established by independently scoring 112 GHC styles from a random selection of videos (Cohen's $K = 0.91$) [13].

In addition to the observation sessions, we used focal follows to investigate GHC behaviour in the Chimfunshi chimpanzees. Focal follow sampling [12] started in February 2011 and has yielded 804 h of observation through March 2012 (groups 1–4: 218, 200, 173 and 213 h, respectively). Our focal follow method is composed of daily observations of each group between 8.30 and 11.00 and between 14.30 and 17.00. Focal subjects were selected through systematic, randomized sampling of the chimpanzees' entire enclosure (as seen from the fence line) and chimpanzees were video-recorded for 10 consecutive minutes. During the review process of the focal follow videos, the handclaps by the focal individual or any other individual in view were extracted. The GHC bouts from these videos were analysed and reported separately (see §3).

Additional data were obtained from records from May to August 2007 (41 days of all-occurrence sampling in both groups 1 and 2, minimally 240 h per group). However, since these data were not collected with the same methodology as in 2010 and 2011, only information on the identities of the GHC partners was extracted from this dataset in order to investigate the transmission of GHC behaviour over time.

(c) Grooming handclasp operationalization

McGrew & Tutin [1] operationalized the grooming handclasp as 'a symmetrical postural configuration in which two participants extend an arm overhead and then either one clasps the other's wrist or hand, or both clasp each other's hand. Meanwhile, the other hand engages in social grooming of the other individual's underarm area revealed by the upraised limb, using typical finger movements'. We extended their operationalization by including two more individually scored clasping styles based on the part of the arm or the hand that makes contact with the partner, generating the categories palm, wrist, forearm and other. Almost all possible combinations of these individual styles were observed at least once across groups (table 2). The category 'other' included styles that could not be reliably classified as either palm, wrist or forearm, but were too diffuse to form one distinct category (e.g. elbow, upper arm). A GHC bout was defined by two individuals making bodily contact by means

of one of the above-mentioned GHC styles, ending with the release and lowering of the arms.

(d) Analyses

To test whether frequencies of different GHC styles differed between groups, we used a generalized linear mixed model (GLMM) [14]. GLMMs allow for determining the effects of one or more predictor variables on a response variable while at the same time accounting for non-independence of the response variable owing to repeated observations (e.g. of the same individuals or dyads). In the models, we included group as a fixed effect, and dyad and the two interacting individuals as random effects. To account for potential daily variation in the frequencies of GHC styles, we included day as a further random effect. Furthermore, we included the year and the interaction between group and year as fixed effects into the model in order to test whether group differences were stable over time. Finally, in the models exploring group differences in GHC style, we only included dyads that engaged in the GHC behaviour at least five times for the reason that an investigation of relative preferences necessitates repeated measures within the same dyad. As the binary response, we first chose the most commonly expressed symmetrical GHC style ('palm-to-palm'; figure 1*a*) as opposed to any other style. In a second model, we additionally investigated the expression of the second most commonly expressed symmetrical GHC style ('wrist-to-wrist'; figure 1*b*).

A separate model tested whether the GHC style symmetry was influenced by the arm-length differential between the clasping partners. Measures of arm lengths were obtained for 27 subjects by photographing chimpanzees reaching for a 30 cm piece of sugar cane through the bars of their indoor holding space and assessing arm length digitally. Inter-observer reliability was established by a second individual independently scoring 100 per cent of the available photos (Pearson correlation: $r = 0.97$, $n = 76$). This model contained the same random effects as the previous models, but included neither year nor the interaction between group and year, and dyads were included even if they had engaged in fewer than five handclasp bouts. Moreover, the response variable comprised the symmetry versus asymmetry of the dyadic GHC style (e.g. palm-to-palm, symmetrical; palm-to-wrist, a-symmetrical). Crucially, the model included the absolute difference between the arm lengths of the two partners as a fixed effect.

Importantly, since the assignment of the two grooming individuals to the two random effects was completely arbitrary, in all models, we randomized this assignment 1000 times and averaged the results of the corresponding 1000 GLMMs. GLMMs were implemented in R [15] using the function `lmer` of the R package `lme4` [16] with binomial error structure and logit link function.

For the analyses on the expansion of the GHC behaviour, we focused on all juveniles that reached the age of the youngest chimpanzee that has been reported to engage in the GHC behaviour (5 years and 9 months [4]) during our data collection (2007–2011).

3. RESULTS

(a) Variation in grooming handclasp style

Two of the four study groups were observed to engage in the GHC behaviour during the observation sessions



Figure 1. Grooming handclasp style examples: (a) palm-to-palm and (b) wrist-to-wrist.

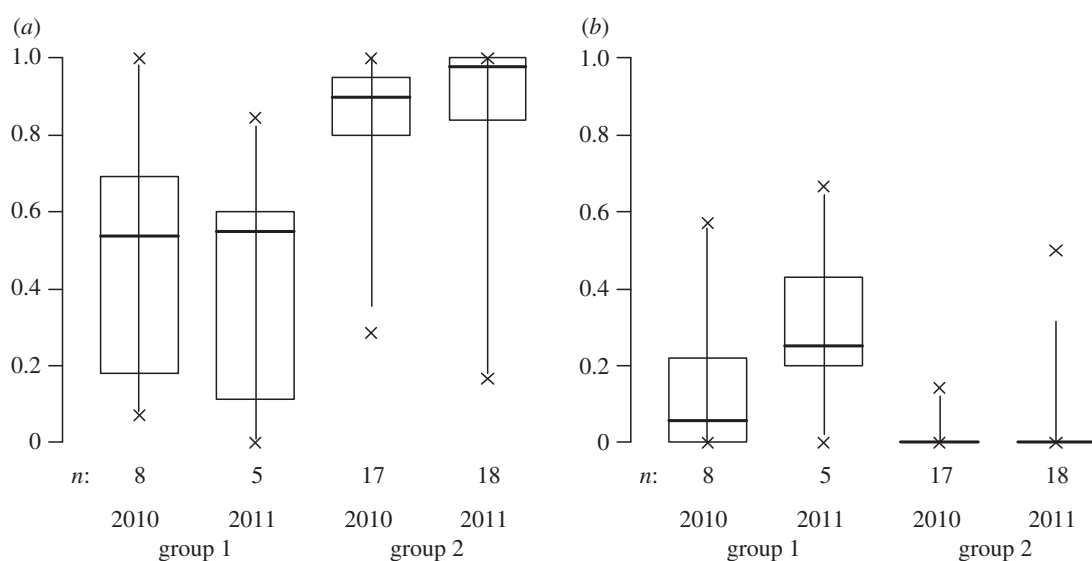


Figure 2. Proportion by which (a) palm-to-palm and (b) wrist-to-wrist GHC styles were used, separately per year and group. n refers to the number of dyads (only dyads with at least five GHC bouts included). Sample sizes for this analysis were 619 GHC bouts and 42 subjects. Shown are medians (thick horizontal lines), quartiles (boxes), percentiles (2.5 and 97.5%, vertical lines) and minimum and maximum (laying crosses) of the proportions per dyad.

in 2010 and 2011 (group 1 and 2); no GHC bouts were observed in the other two groups (group 3 and 4). Overall rates of GHC bouts in group 1 and 2 during the observation sessions were 4.7 ($n = 163$) and 11.7 bouts h^{-1} ($n = 410$) in 2010, and 1.7 ($n = 61$) and 15.4 bouts h^{-1} ($n = 538$) in 2011, respectively. In 811 of the 1172 observed GHC bouts, we were able to identify GHC style for both partners (table 2).

Crucially, there were marked group differences in the frequencies with which the palm-to-palm and wrist-to-wrist styles were used (figure 2). The palm-to-palm style was significantly more frequent in group 2 ($p = 0.008$, $\beta = 1.86$, $s.e. = 0.70$, $n = 619$), while the wrist-to-wrist style was significantly more frequent in group 1 ($p = 0.015$, $\beta = -3.05$, $s.e. = 1.25$, $n = 619$; both tests derived from models not comprising the interaction; see below). The interaction between year and group was not significant in the wrist-to-wrist model ($p = 0.763$, $\beta = -0.72$, $s.e. = 2.35$, $z = -0.30$), but tended to be so in the palm-to-palm model ($p = 0.069$, $\beta = 1.36$, $s.e. = 0.74$, $z = 1.83$). Inspection of the results

suggested that the group differences did not change strongly over the course of 2010–2011 (figure 2).

Another 59 GHC bouts for group 1 and 160 GHC bouts for group 2 were observed during focal follow sampling. We were able to identify the GHC styles for both partners in 53 cases involving 17 subjects in group 1 and 143 cases involving 31 subjects in group 2. The focal follow data revealed the same pattern as the data collected during the observation sessions in 2010 and 2011. The percentage of GHC bouts that were palm-to-palm in group 2 was higher than in group 1 (group 2, 90.2%; group 1, 13.2%). The percentage of GHC bouts that were wrist-to-wrist was greater in group 1 than in group 2 (group 1, 49.1%; group 2, 1.4%). While no GHC bouts have been observed in group 3 since the formation of this group in 1995, four individuals in this group were observed to engage in GHC behaviour during the focal follow period, resulting in three bouts in total (first bout in September 2011). Given the low frequency of occurrence, however, the GHC behaviour in group 3 was not subject to analysis. Notably, group 4 was never

observed to engage in GHC behaviour—not during the observation sessions, nor during the focal follow period.

(b) Influence of arm-length differential on grooming handclasp style

The symmetry of the dyadic handclasp styles was not predicted by the absolute arm-length differential of the clasping partners ($p = 0.61$, $n = 321$ GHC bouts, 27 subjects, 53 dyads).

(c) Durability of the grooming handclasp behaviour

Based on personal observations (M. Bodamer 2003–2012) and personal communication with the chimpanzee keepers (P. Chambatu 2011), we can conservatively state that the GHC behaviour has been part of the behavioural repertoire of the Chimfunshi chimpanzees in groups 1 and 2 for at least 9 years.

(d) Expansion of the grooming handclasp behaviour

The assessment of the GHC transmission showed that 20 juveniles (11 females) out of the 23 juveniles in the handclasp groups (11 females) started engaging in the GHC behaviour and that in 83 per cent of the possible cases the mother was the first partner of these new handclaspers (see the electronic supplementary material, table S1).

4. DISCUSSION

This study shows that groups of chimpanzees that do not systematically differ in their genetic backgrounds and live in similar ecological environments can execute social behaviour in group-specific ways. The group differences in GHC style preferences were robust and consistent over time, augmenting the argument that the GHC behaviour provides an example of chimpanzees' capacity to adopt, maintain and transmit a group-specific behaviour that is social in nature [1]. The emergence of the GHC behaviour in group 3 supports our interpretation of GHC behaviour being a behavioural phenomenon that has the propensity to emerge naturally in chimpanzee groups, and reinforces the need for detailed analyses such as these that go beyond the presence–absence distinction to evaluate whether the behaviour occurs in varying styles across groups. Observations that the GHC behaviour spreads to naive individuals and that the first partner of new handclaspers is most often the mother is consistent with previous research [4], and provides evidence for the primary line of behavioural transmission in chimpanzees being along maternal lines.

Based on a large dataset, our results show that neighbouring groups of chimpanzees can differ in their social grooming behaviour. The finding that only two groups regularly engaged in GHC behaviour, while this behaviour was (nearly) absent in the other two groups, validates the original study by McGrew & Tutin [1]. Furthermore, the finding that the neighbouring groups, of chimpanzees have different GHC style preferences validates the more detailed studies by Nakamura & Uehara [3] and McGrew *et al.* [11]. Importantly, the use of mixed models allows us to draw the conclusion that the group-specific style preferences were shared by most individuals within the respective groups, thus controlling for individual and dyadic preferences that could have influenced the results

in the studies on the Mahale chimpanzees [3,11]. In more detail, the *variation* of the GHC behaviour was robust in the sense that over the course of 2010–2012, the only two groups that engaged in the GHC behaviour showed stable differences in their style preferences. This result was found by comparing the chimpanzees' preferences at two different points in time (1-year interval) using a large number of observations and was corroborated by the observations of the year-round data collection procedure. Furthermore, the GHC behaviour has been observed for more than 9 years in the Chimfunshi chimpanzees, indicating that the GHC behaviour is a stable part of the behavioural repertoire of the chimpanzees under study and surpassing the *durability* criterion [6]. More importantly, the criterion of *expansion* has also been satisfied in this study as the results showed that the GHC behaviour spread to formerly naive subjects over time—in this case from one generation to the next (most often from mother to offspring). The dyadic nature of the GHC behaviour additionally indicates that GHC behaviour is not merely a behaviour that was individually discovered and maintained within one generation, but instead gets actively transmitted by means of social learning. The exact way in which the GHC behaviour gets transmitted, however, remains unclear. Where mothers have been observed to raise one arm of their offspring with one of their own arms in a way that resembles the GHC posture (but without an active clasping role of the offspring), these interactions have also been observed in the non-handclasp group (K. A. Cronin & E. J. C. van Leeuwen 2011, personal observation). Moreover, long-term observations are needed to elucidate how the group-specific preferences are transmitted and maintained over time. Interestingly, the group preferences reported here were already existent in 2007 (M. Bodamer & E. J. C. van Leeuwen, unpublished data). In conjunction with the fact that, over the course of 2007–2011, the composition of one of the GHC groups has changed such that five handclasp individuals are no longer present in this group, this further indicates that the GHC preferences are not limited to certain individuals, but rather shared by (most individuals in) the group.

Recently, chimpanzees have been shown to exhibit group-specific preferences for nut-cracking techniques [17]. While traditions and cultures have been difficult to establish in animal societies because of confounding ecological and genetic factors [7,18–19], this study reports on group differences in nut-cracking behaviour within the same subspecies of chimpanzees, while at the same time controlling for the most important environmental determinants [17]. The present study similarly reports on behavioural differences between neighbouring groups of chimpanzees, yet in the realm of social interactions instead of tool-use behaviour. Any ecological or genetic factor is unlikely to fully account for the findings of the present study for the following reasons: first, the four groups under study live in the same miombo forest and second, the groups do not systematically differ in their genetic composition. More importantly, the group differences comprised *relative* preferences, meaning that all the GHC styles were in the behavioural repertoires of the two handclasp groups and thus that genetic influences on our results can be ruled out even more compellingly. Finally, one important physical property of this social

grooming behaviour (the arm-length differential) did not predict GHC style.

In this study, we have evaluated our findings against criteria that have been developed in order to decrease the likelihood that the behaviour under study is determined by non-social aspects, such as genetics and environment, and increase the likelihood that the behaviour under study is group-specific and socially transmitted [6,10]. Based on this scrutiny, we conclude that chimpanzees' social behaviour is not only motivated by innate predispositions and individual inclinations, but may also be partly cultural in nature.

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REFERENCES

- 1 McGrew, W. C. & Tutin, C. E. G. 1978 Evidence for a social custom in wild chimpanzees? *Man* **13**, 234–251. (doi:10.2307/2800247)
- 2 de Waal, F. B. M. & Seres, M. 1997 Propagation of handclasp grooming among captive chimpanzees. *Am. J. Primatol.* **43**, 339–346. (doi:10.1002/(SICI)1098-2345(1997)43:4)
- 3 Nakamura, M. & 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. (doi:10.1086/381007)
- 4 Bonnie, K. E. & De Waal, F. B. M. 2006 Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates* **47**, 27–34. (doi:10.1007/s10329-005-0141-0)
- 5 Humle, T., Colin, C. & Raballand, E. 2009 Preliminary report on hand-clasp grooming in sanctuary-released chimpanzees, Haut Niger National Park, Guinea. *Pan Afr. News* **16**, 7–10.
- 6 Perry, S. *et al.* 2003 Social conventions in wild white-faced capuchin monkeys—evidence for traditions in a neotropical primate. *Curr. Anthropol.* **44**, 241–258. (doi:10.1086/345825)
- 7 Whiten, A. & Van Schaik, C. P. 2007 The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)
- 8 Webster, T. H., Hodson, P. R. & Hunt, K. D. 2009 Grooming hand-clasp by chimpanzees of the Mugiri community, Toro-Semliki Wildlife Reserve, Uganda. *Pan Afr. News* **16**, 5–7.
- 9 Goodall, J. 1968 The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* **1**, 161–311.
- 10 Whiten, A. 2003 Peer commentary on S. Perry *et al.* 2003 Social conventions in wild white-faced capuchin monkeys—evidence for traditions in a neotropical primate. *Curr. Anthropol.* **44**, 260–261.
- 11 McGrew, W. C., Marchant, L. F., Scott, S. E. & 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. (doi:10.1086/318441)
- 12 Martin, P. & Bateson, P. 2007 *Measuring behaviour: an introductory guide*, 3rd edn. Cambridge, UK: Cambridge University Press.
- 13 Cohen, J. 1960 A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* **20**, 37–46. (doi:10.1177/001316446002000104)
- 14 Baayen, R. H. 2008 *Analyzing linguistic data*. Cambridge, UK: Cambridge University Press.
- 15 R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- 16 Bates, D., Maechler, M. & Bolker, B. 2011 lme4: linear mixed-effects models using S4 classes. R package v. 0.999375-42. See <http://cran.r-project.org/web/packages/lme4/index.html>.
- 17 Luncz, L. V., Mundry, R. & Boesch, C. 2012 Evidence for cultural differences between neighboring chimpanzee communities. *Curr. Biol.* **22**, 922–926. (doi:10.1016/j.cub.2012.03.031)
- 18 Laland, K.N. & Galef, B.G. 2009 *The question of animal culture*. Cambridge, MA: Harvard University Press.
- 19 McGrew, W. C. 2004 *The cultured chimpanzee: reflections on cultural primatology*. Cambridge, UK: Cambridge University Press. (doi:10.2277/0521535433)