Genetic and 'cultural' similarity in wild chimpanzees

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Genetic similarity and ‘cultural’ similarity in wild chimpanzees

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Summary Research interest in the importance of group-specific, socially transmitted behaviour (i.e., ‘cultures’ or ‘traditions’) in the lives of animals has increased in recent years, partly as a result of high profile reports of extensive variation in the behavioural repertoires of wild animals. The current dominant approach to identifying animal culture in the wild, which infers the existence of culture by eliminating ecological explanations for differences in the behavioural repertoires of groups, was first applied to chimpanzees. Some critics, however, argue that genetic differences between groups have not yet been ruled out as a factor contributing to differences in the behaviour of groups of chimpanzees and other animals. Here we examined this issue directly by combining genetic and behavioural data from nine groups of wild chimpanzees. We found that genetic differentiation among chimpanzees, at both the between-subspecies and within-subspecies level, cannot be ruled out as playing a major role in generating group differences in behaviour. We also found that behaviours involved in non-vocal communication may be more likely to represent true cultural variants, as the distribution of these types of behaviours fit the predictions of the genetics hypothesis less well than did other types of behaviours.
The importance of group-specific, socially transmitted behaviour to the lives of non-human animals, and its relevance to the evolution of human culture, is a matter of considerable controversy (Galef and Heyes 1996; Boesch 2003; Laland and Janik 2006; Laland and Galef 2009). As our closest living relatives and the most intensively-studied non-human primate in the wild, chimpanzees have played a particularly important role in the study of animal culture (Goodall 1973; McGrew 1992; Boesch 1996; Boesch and Tomasello 1998). A landmark survey of geographic variation in chimpanzee behaviour found 39 behaviours, including various forms of tool use, grooming, and courtship behaviour, that were common in at least one chimpanzee group but absent in at least one other, and for which an ecological explanation for this absence was judged to be unlikely, (e.g., a lack of ‘termite fishing’ even though the appropriate termite species was present) (Whiten et al. 1999; Whiten et al. 2001). This so-called “method of exclusion”, which infers the existence of culture by eliminating ecological explanations for the patterning of between-group behavioural variation, has since been applied to several other primate and non-primate species, and is now the dominant approach used to identify animal culture in the wild (Rendell and Whitehead 2001; Hohmann and Fruth 2003; Perry et al. 2003; van Schaik et al. 2003).

In a pattern reminiscent of between-group variation in human behaviour, each chimpanzee group had its own unique combination of these putative cultural variants. This complex, mosaic pattern of between-group variation in behaviour was very different than that observed in prior studies of animal culture, where in most cases only one type of behaviour varied among groups (e.g., bird song dialect (Marler and Tamura 1964)). Despite various other species showing patterns of behavioural diversity that approach
levels shown in chimpanzees, for many, chimpanzees remain “the prime exemplar of animal culture” (Boesch 2003; McGrew 2004; Laland et al. 2009).

Research conducted in captivity shows that chimpanzees have the requisite social learning abilities to produce stable differences in group-specific behaviour (Whiten et al. 2005; Horner et al. 2006; Bonnie et al. 2007; Whiten et al. 2007; Price et al. 2009). In one experiment (Whiten et al. 2005), for example, two chimpanzees were isolated from their respective groups and trained in alternative techniques to use a tool to gain access to food in an experimental apparatus. These two “demonstrators” were then re-introduced into their original groups, whose behaviour was then compared with each other and with that of a third group who had no such access to a trained demonstrator. Chimpanzees in the first two groups predominately performed the technique of their demonstrator, while chimpanzees in the third group did not learn to gain access to the food.

However, although the social learning abilities of chimpanzees are sufficient to produce group differences in behaviour, this does not necessarily indicate that all or even most of the behavioural variants observed in the wild arise as a result of social learning, and thus represent true cultural variants (Galef 1990; Tomasello 1990; Boesch 1996; Galef 2009; Laland et al. 2009). Some critics argue that insufficient attention has been paid to the possibility that genetic differences are responsible for behavioural variation between chimpanzee groups (Galef 1990; Heyes 1994; Heyes and Galef 1996; Laland et al. 2006; Tennie et al. 2009). Recent research showing that individuals raised with no opportunity to acquire the behaviour through social learning nevertheless exhibit sophisticated abilities to use tools (crows) (Kenward et al. 2005) and process foods (gorillas) (Tennie et al. 2008) suggests that complex behaviours can at least partly be
under genetic control, and thus that group differences in the underlying genetic
predispositions and abilities could plausibly contribute to group differences in behaviour. Indeed, almost one-third of the putative cultural variants in the original report (Whiten et al. 1999) of geographical variation in chimpanzee behaviour are found only in Pan troglodytes verus, the most genetically divergent of the four chimpanzee subspecies, and considered by some to represent a different species (Morin et al. 1994; Gagneux et al. 1999).

In the only systematic investigation of this issue, Lycett and colleagues (Lycett et al. 2007; Lycett et al. in press) reasoned that if the patterning of intergroup variation in behaviour is primarily the product of genetic differences between subspecies, then a tree of the relationships between chimpanzee groups generated from a cladistic analysis of the 39 putative cultural variants should have more phylogenetic structure when two subspecies are considered together than a tree generated from the East African subspecies alone. They failed to find more phylogenetic structure in the two-subspecies than the single-subspecies tree, and thus concluded that the patterning of between-group variation in chimpanzee behaviour fit a cultural explanation better than a genetic one.

While an important first step towards an explicit investigation of the role of genetic differentiation in generating intergroup variation in behaviour, this study has four major limitations. First, as acknowledged by Lycett and colleagues (Lycett et al. in press), at present there is no well-accepted statistical methodology for comparing the extent of phylogenetic structure in two different trees. Second, recent simulation studies show that measures of phylogenetic structure are very sensitive to rates of evolution (Nunn et al. in press). Even if the behavioural variants were genetically determined, then
a sufficiently high rate of evolution, which could be caused by selection, could produce a lower signal of phylogenetic structure in a tree with deeper phylogenetic separation (Nunn et al. in press). Third, the one-subspecies versus two-subspecies analysis presupposes that only genetic differentiation between subspecies, but not genetic differentiation among groups within a single subspecies, can affect behavioural variation among groups. Although the statement that “populations within East Africa cannot be distinguished” (Lycett et al. 2007) p. 17589 is technically correct in the sense that there is sharing of mitochondrial DNA (mtDNA) haplotypes across the subspecies range, quantitative analyses show that there is as much geographical structuring of genetic variation within the East African subspecies as within the entire human species (Goldberg and Ruvolo 1997). That the extent of genetic differentiation among chimpanzee groups belonging to the same subspecies is sufficient to affect between-group behavioural variation is suggested by the finding that genetically influenced variation in body size is implicated in differences between the qualities of vocalizations of two groups of chimpanzees belonging to the same East African subspecies (Mitani et al. 1999). Finally, the method employed by (Lycett et al. 2007; Lycett et al. in press) purports to test only whether genetics can be excluded as a cause for overall levels of similarity in the behavioural repertoires of chimpanzee groups; it offers no insight into how strongly the distribution of each of the individual behavioural variants follows (or does not follow) patterns of between-group genetic differentiation. Some authors have suggested that differences in non-vocal communicative behaviours are particularly unlikely to result from differences in underlying genetic predispositions, as this class of behaviours is less likely than other classes of behaviour (e.g., tool-use in a foraging context) to be
influenced by the differential operation of natural selection according to local ecological conditions (Boesch 1996; van Schaik 2009).

Here we take a more direct approach to the question of whether genetics can be excluded as playing a role in generating intergroup variation in the behaviour of wild chimpanzees by measuring levels of genetic differentiation among nine groups of wild chimpanzees (three from the West African *P. t. verus* and six from the East African *P. t. schweinfurthii* subspecies), and comparing these results with patterns of between-group behavioural variation. Our study involved five steps. First, we sequenced most of the members of each of the nine groups at the first hypervariable region of the maternally inherited mtDNA and estimated levels of between-group genetic similarity/differentiation. Second, we converted the behavioural data of the original study of geographical variation in chimpanzee behaviour (Whiten et al. 1999) (as well as data from two newly assessed chimpanzee groups) into numerical codes reflecting how frequently each of the 39 behaviours occurred in each chimpanzee group. Third, we used these behavioural data to generate, for each of the 36 pairs of groups, (1) a measure of the overall level of behavioural similarity (*sensu* (Lycett et al. 2007; Lycett et al. in press)), and (2) a measure of the level of differentiation for each of the individual behavioural variants. Fourth, we examined how well patterns of between-group genetic variation matched patterns of between-group (1) overall behavioural similarity and (2) differentiation for each of the individual behavioural variants. And fifth, we tested whether the pattern of between-group genetic differentiation predicted patterns of between-group behavioural differentiation less well for behavioural variants involved in non-vocal communication than it did for other types of behavioural variants.
Results and Discussion

We found that the overall level of genetic differentiation among the 9 groups was substantial (AMOVA value = 0.49, $p = 0.00001$), and that the majority of pairs of groups (28 / 36 = 77.8%) were significantly genetically differentiated from one another (Table 1). Of the 12 pairs of groups showing no significant genetic differentiation, three were located in the same block of continuous forest (Mahale K and M, Kibale Kanayawara and Ngogo, Taï North and South), and four involved pairs that contained the poorly genetically sampled Mahale K group.

When comparing the genetic and behavioural data, we found that levels of genetic similarity and levels of overall behavioural similarity between chimpanzee groups were strongly and significantly correlated (Pearson matrix permutation correlation, $N = 26$ pairs, $R = 0.59, p = 0.001$) (figure 1; table 1). The relationship between genetic similarity and overall behavioural similarity was less strong and failed to reach statistical significance when calculated for the much smaller data set of only the 6 groups belonging to the East African subspecies (Pearson matrix permutation correlation, $N = 15$ pairs of groups, $R = 0.35, p = 0.18$). These results suggest that genetic differentiation cannot be excluded as an explanation for overall patterns of behavioural variation among chimpanzees, and may even play a role in generating behavioural variation among groups within a single subspecies.

The strong correlations between genetic and overall behavioural similarity, however, do not necessarily preclude social learning as contributing to the patterning of behavioural variation among chimpanzee groups. If emigrating females carry the
behavioural variants of their natal group to their new group, then groups that share more
migrants are likely to be more behaviourally similar. High migration rates between
groups could thus result in a positive correlation between genetic and behavioural
similarity, even if behavioural variants were completely socially learned. It is thus only
when patterns of behavioural and genetic similarity are discordant that inferences can be
made about the role of social learning in generating geographical variation in behaviour.

Our second goal was therefore to identify those behavioural variants whose
geographical distribution did not match the predictions of the genetic hypothesis,
suggesting they represent true socially learned cultural variants. We found that the
individual behavioural variants varied continuously in the extent to which their
distribution matched patterns of genetic differentiation (table 2). The combination of a
relatively modest sample size (N = 6 to 36 pairs of groups) and the stringent alpha level
(e.g., in this case, a Bonferroni correction of 0.05 / 24 = 0.002) that is required to correct
for multiple comparisons means that there is very low power to reject the null hypothesis
that the distribution of each behavioural variant is predicted by genetic differentiation.
Thus, it is not possible to make strong inferences about which of the individual
behavioural variants can and which of the individual behavioural variants cannot be
excluded as being explained by patterns of genetic differentiation.

However, we did find that, as a whole, the distribution of non-vocal
communicative behavioural variants was less well predicted by patterns of genetic
differentiation than was the distribution of the other types of behavioural variants (table
2, figure 2). The mean of the Spearman rank correlation coefficients between behavioural
differentiation and genetic differentiation was significantly higher among the
communicative behavioural variants ($\bar{X} = 0.01$, 95 % C.I. = 0.07) than among the non-
communicative behavioural variants ($\bar{X} = 0.22$, 95 % C.I. = 0.11) (independent samples t
test; $t (29.3) = 3.234, p = 0.003$).

Conclusions

Here we have shown that genetic differences cannot be excluded as playing a
major role in structuring patterns of behavioural variation among chimpanzee groups,
particularly for behaviours not involved in non-vocal communication. As others have
noted, the method of exclusion may lead to an underestimation of the true number of
cultural variants that exist in the wild (Boesch 1996; Laland et al. 2006; Laland et al.
2009). Our results showing that chimpanzee groups separated by more than $\approx 300$ km are
likely to show significant genetic differentiation suggests that if the method of exclusion
is strictly applied, then only behaviours that vary among chimpanzee groups that are very
geographically close should be considered as cultural variants (e.g. (Mobius et al. 2008)).

It has been proposed (Lefebvre 1995; Franz and Nunn 2009; Kendal et al. 2009) that
mathematical methods to identify a statistical ‘signature’ of transmission of a behavioural
variant through social learning are a promising way to investigate culture in the wild for
animals, like chimpanzees, where definitive translocation experiments (e.g. (Helfman and
Schultz 1984)) are impossible for logistic and ethical reasons. Unfortunately, while we
often have a good understanding of the distribution of a behaviour among the individuals
within a group, the diffusion processes that led to that distribution are rarely observed
(Perry et al. 2003). Comparing patterns of behavioural variation with patterns of kinship
among individuals within the same social group may be a more tractable way to
investigate animal culture in the wild (Krutzen et al. 2005), particularly in species like chimpanzees where the relatively weak influence of kinship on patterns of affiliation (Langergraber et al. 2007; Langergraber et al. 2009) means that evidence for social learning (i.e., animals that interact with each other more frequently are more likely to share the behavioural variant) is not confounded with evidence for genetic inheritance (i.e., close relatives are more likely to share the behavioural variant). In sum, diverse methodologies will be essential to resolving the long-standing debate of the relative contributions of genetics, social learning, and other factors in generating geographical variation in animal behaviour.

**Materials and Methods**

We examined mitochondrial (mtDNA) variation (354 bases of the first hypervariable region) in nine groups of chimpanzees (numbers of adolescent and adult individuals sequenced / number of adolescent and adult group members present at time of sampling in brackets): the Bossou group (12/12) of Guinea, the North (8/11) and South (16/26) groups of Taï National Park, Cote d’Ivoire, the Sonso group (28/28) of Budongo Forest Reserve, Uganda, the Ngogo (89/89) and Kanyawara (20/20) groups of Kibale National Park, Uganda, the M (32/32) and K (3/Unknown) groups of Mahale Mountains National Park, Tanzania, and the Kasekela (38/38) group of Gombe Stream National Park, Tanzania. mtDNA sequences for five of the groups were previously published: Bossou (Shimada et al. 2009), Sonso (Langergraber et al. 2007), Gombe (Liu et al. 2008), Ngogo (Langergraber et al. 2007), Kanyawara (Langergraber et al. 2007). We
generated new mtDNA sequences for the Taï North and South groups, the Mahale M and K groups, and the Gombe Kasekela group, following previously described procedures [24, 25]. The Genbank (http://www.ncbi.nlm.nih.gov) accession numbers for the chimpanzee mtDNA sequences used in this study are EU077270-EU077418, XXXXXXXX-XXXXXXXX, and XXXXXXXX-XXXXXXXX.

AMOVA and pairwise $F_{ST}$ values were calculated using Arlequin 3.1 (Excoffier et al. 2005), with genetic distances between haplotypes measured using the number of nucleotide differences, and statistical significance was assessed by comparison with genetic differentiation calculated on random data sets where mtDNA haplotypes were permuted among groups. Although mtDNA is unlikely to directly code for any of the behavioural variants considered here, it is an excellent marker for determining overall levels of genetic similarity among groups, particularly in species such as chimpanzees where females rather than males move between groups. This is supported by the strong correlation between mtDNA genetic distance and geographical distance among the nine chimpanzee groups included in this study (Pearson correlation matrix permutation, $N = 36$ pairs of groups, $R = 0.96$, $p = 0.00005$).

For six of the chimpanzee groups in this study (Bossou, Sonso, Kanyara, Mahale M and K, Kasekela), we used the behavioural codes as described in the original paper on geographical variation in chimpanzee behaviour (Whiten et al. 1999; Whiten et al. 2001). For Taï North we changed three codes from the original paper, as one of us (C.B., the director of this field site) decided that these new codes were more accurate: ‘Hand-clasp’ was changed from habitual to present, ‘Knuckle-knock’ was changed from customary to habitual, and ‘Branch-slap’ was changed from customary to absent. We repeated our
analyses of the relationship between overall behavioural and genetic similarity using the original codes for Taï North and found no qualitative changes in our results (Pearson correlation matrix permutation, $N = 36, R = 0.61, p = 0.001$). Taï South group, newly coded for this study by C.B., had the same codes as Taï North, with the following two exceptions: ‘Bee-probe’ was coded as present and ‘Marrow-pick’ as habitual. Ngogo, newly coded by J.M. and K.L. for this study, had the same codes as Kanyawara, with the following two exceptions: ‘Seat-vegetation’ was coded as habitual, and ‘Leaf-clip, mouth’ was coded as customary. The behavioural variant ‘Branch-din’ was excluded from all analyses because it was absent in all nine of the chimpanzee groups included in this study. Thus, our study examined only 38 of the 39 putative cultural variants described in the original study on geographical variation in chimpanzee behaviour (Whiten et al. 1999; Whiten et al. 2001). We made no attempt to include behaviours now known or suspected to vary between chimpanzee groups that were not included in this original study (e.g., ‘social scratch’ (Nishida et al. 2004)).

We converted the behavioural codes into numbers as follows: (3) ‘customary’, the behaviour occurs in all or most able-bodied members of at least one age-sex class (such as adult males); (2) ‘habitual’, the behaviour is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (1) ‘present’, the behaviour is neither customary nor habitual but is clearly identified; (0) ‘absent’, the behaviour has not been recorded and no ecological explanation is apparent; (?) ‘ecological explanation’, absence is explicable because of a local ecological feature; and (?!) ‘unknown’, the behaviour has not been recorded, but this may be due to inadequacy of relevant observational opportunities. Our numerical coding system differs from that used
in the study of Lycett and colleagues (Lycett et al. 2007; Lycett et al. in press), in that these authors did not distinguish between behavioural variants that were absent and those that were absent due to an ecological reason, coding both types as 0.

We then used these data to calculate Pearson correlations between each of the 36 pairs of chimpanzee groups, giving a measure of overall behavioural similarity that could potentially range from -1 to 1. We compared this matrix of overall behavioural similarity to the matrix of genetic similarity ($1 - F_{ST}$) using a Pearson matrix correlation test. For the analysis of the relationship between genetic differentiation and the distribution of the individual behavioural variants, we created a matrix consisting of the absolute value of the difference in the numerical code between each of the communities, such that communities that were similar for the behavioural variant had a score of 0 (i.e., both had the same code), and communities that were very different for the behavioural variant had a score of 3 (i.e., ‘habitual’ in one group and ‘absent’ in the other). We then calculated a Spearman rank correlation matrix permutation test between each of these 38 matrices and a matrix of genetic differentiation ($F_{ST}$). The independent samples t-test we used to compare the average of the Spearman rank correlations between behavioural differentiation and genetic differentiation of the communicative and non-communicative behaviours accounted for unequal variances between these two groups (Levene’s test for equality of variance, $F = 5.159$, $p = 0.03$). This independent samples t-test was computed on the 34 behavioural variants where at least 15 pairs of groups did not have a missing value (i.e., ‘ecological explanation’ or ‘unknown’).

All matrix permutation tests used 10,000 permutations.
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Table and Figure Captions

Figure 1. The relationship between levels of overall behavioural similarity and levels of genetic similarity in 36 pairs of wild chimpanzee groups.

Table 1. Genetic similarity (below diagonal) and overall behavioural similarity (above diagonal) in 36 pairs of chimpanzee groups. Pairs where genetic differentiation is statistically significantly different from 0 are in listed in bold.

Table 2. Spearman rank correlations between behavioural distance and genetic distance for the individual behavioural variants. Also shown are the classifications of behavioural variants as non-vocal communicative or not. Behavioural variants are listed in descending order of strength of negative correlation with genetic distance.
Figure 2. Mean of the correlation coefficients between genetic and behavioural
differentiation for non-vocal communicative and other types of behavioural variants.
Error bars represent 95% confidence intervals.

References


Horner, V., Whiten, A., Flynn, E. & de Waal, F. B. M. 2006 Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and


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<th>Gombe Kasekela</th>
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<tr>
<td>Leaf-dab (leaf dabbed on wound, examined)</td>
<td>36</td>
<td>-0.03</td>
<td>0.82</td>
<td>no</td>
<td></td>
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<tr>
<td>Leaf-strip (rip leaves off stem, as threat)</td>
<td>36</td>
<td>-0.02</td>
<td>0.88</td>
<td>yes</td>
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<tr>
<td>Fly-whisk (leafy stick used to fan flies)</td>
<td>21</td>
<td>0.00</td>
<td>0.99</td>
<td>no</td>
<td></td>
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</tr>
<tr>
<td>Food-pound onto other (e.g., stone)</td>
<td>21</td>
<td>0.00</td>
<td>0.99</td>
<td>no</td>
<td></td>
<td></td>
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<tr>
<td>Stem pull-through (pull stems noisily)</td>
<td>36</td>
<td>0.00</td>
<td>0.99</td>
<td>yes</td>
<td></td>
<td></td>
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<tr>
<td>Expel/stir stick expels or stirs insects</td>
<td>21</td>
<td>0.02</td>
<td>0.93</td>
<td>no</td>
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<tr>
<td>Branch-slap (slap branch, for attention)</td>
<td>36</td>
<td>0.03</td>
<td>0.82</td>
<td>yes</td>
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<td></td>
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<tr>
<td>Ant-fish (probe used to extract ants)</td>
<td>36</td>
<td>0.03</td>
<td>0.78</td>
<td>no</td>
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<tr>
<td>Aimed-throw (throw object directionally)</td>
<td>36</td>
<td>0.06</td>
<td>0.60</td>
<td>no</td>
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<tr>
<td>Shrub-bend (squash stems underfoot)</td>
<td>36</td>
<td>0.07</td>
<td>0.63</td>
<td>yes</td>
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<tr>
<td>Lever open (stick used to enlarge entrance)</td>
<td>36</td>
<td>0.10</td>
<td>0.58</td>
<td>no</td>
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<tr>
<td>Fluid-dip (use of probe to extract fluids)</td>
<td>36</td>
<td>0.14</td>
<td>0.31</td>
<td>no</td>
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<tr>
<td>Bee-probe (disable bees, flick with probe)</td>
<td>36</td>
<td>0.15</td>
<td>0.35</td>
<td>no</td>
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<tr>
<td>Knuckle-knock (knock to attract attention)</td>
<td>36</td>
<td>0.16</td>
<td>0.28</td>
<td>yes</td>
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<tr>
<td>Hand-clasp (clasp arms overhead, groom)</td>
<td>36</td>
<td>0.18</td>
<td>0.20</td>
<td>no</td>
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<tr>
<td>Club (strike forcefully with stick)</td>
<td>36</td>
<td>0.24</td>
<td>0.10</td>
<td>no</td>
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<tr>
<td>Leaf-napkin (leaves used to clean body)</td>
<td>36</td>
<td>0.25</td>
<td>0.10</td>
<td>no</td>
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<tr>
<td>Nut-hammer, wood hammer on stone anvil</td>
<td>15</td>
<td>0.28</td>
<td>0.24</td>
<td>no</td>
<td></td>
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<tr>
<td>Nut-hammer, other (e.g., on ground)</td>
<td>15</td>
<td>0.28</td>
<td>0.24</td>
<td>no</td>
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<tr>
<td>Food-pound onto wood (smash food)</td>
<td>21</td>
<td>0.35</td>
<td>0.07</td>
<td>no</td>
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<tr>
<td>Index-hit (squash ecto-parasite on arm)</td>
<td>36</td>
<td>0.35</td>
<td>0.05</td>
<td>no</td>
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<tr>
<td>Marrow-pick (pick bone marrow out)</td>
<td>36</td>
<td>0.39</td>
<td>0.04</td>
<td>no</td>
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<tr>
<td>Rain dance (slow display at start of rain)</td>
<td>36</td>
<td>0.39</td>
<td>0.03</td>
<td>no</td>
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<td>Seat-vegetation (large leaves as set)</td>
<td>36</td>
<td>0.49</td>
<td>0.02</td>
<td>no</td>
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<td>Leaf-groom (intense 'grooming' of leaves)</td>
<td>36</td>
<td>0.72</td>
<td>0.01</td>
<td>no</td>
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<tr>
<td>Ant-dip-single (one handed dip stick on ants)</td>
<td>36</td>
<td>0.84</td>
<td>0.00</td>
<td>no</td>
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<tr>
<td>Nut-hammer, stone hammer on stone anvil</td>
<td>15</td>
<td>0.85</td>
<td>0.02</td>
<td>no</td>
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</table>
Figure 1.