Genetic and 'cultural' similarity in wild chimpanzees

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1   **Genetic similarity and 'cultural' similarity in wild chimpanzees**

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3   Kevin Langergraber[1*], Christophe Boesch[1], Eiji Inoue[2], Miho Inoue-Muruyama[3], John

4   Mitani[4], Toshisada Nishida[5], Anne Pusey[6], Grit Schubert[1], Emily Wroblewski[6], Linda

5   Vigilant[1]

6

7   [1]Primatology Department, Max Planck Institute for Evolutionary Anthropology,

8   Deutscher Platz 6, Leipzig 04103, Germany

9   [2]Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan

10   [3]Wildlife Research Center, Kyoto University, Kyoto 606-8203, Japan

11   [4] Department of Anthropology, University of Michigan, 101 West Hall, 1085 South

12   University Avenue, Ann Arbor, MI 48109-1107, USA.

13   [5]Japan Monkey Center, 26 Kanrin, Inuyama 484-0081, Japan.

14   [6]Department of Ecology, Evolution, and Behaviour, University of Minnesota, 100

15   Ecology Building,1987 Upper Buford Circle, St. Paul, MN 55108, USA.

16

17   Author for correspondence (langergr@eva.mpg.de).

18

18   **Summary** Research interest in the importance of group-specific, socially transmitted

19   behaviour (i.e., 'cultures' or 'traditions') in the lives of animals has increased in recent

20   years, partly as a result of high profile reports of extensive variation in the behavioural

21   repertoires of wild animals. The current dominant approach to identifying animal culture

22   in the wild, which infers the existence of culture by eliminating ecological explanations

23   for differences in the behavioural repertoires of groups, was first applied to chimpanzees.

24   Some critics, however, argue that genetic differences between groups have not yet been

25   ruled out as a factor contributing to differences in the behaviour of groups of

26   chimpanzees and other animals. Here we examined this issue directly by combining

27   genetic and behavioural data from nine groups of wild chimpanzees. We found that

28   genetic differentiation among chimpanzees, at both the between-subspecies and within-

29   subspecies level, cannot be ruled out as playing a major role in generating group

30   differences in behaviour. We also found that behaviours involved in non-vocal

31   communication may be more likely to represent true cultural variants, as the distribution

32   of these types of behaviours fit the predictions of the genetics hypothesis less well than

33   did other types of behaviours.

34

34   The importance of group-specific, socially transmitted behaviour to the lives of

35   non-human animals, and its relevance to the evolution of human culture, is a matter of

36   considerable controversy (Galef and Heyes 1996; Boesch 2003; Laland and Janik 2006;

37   Laland and Galef 2009). As our closest living relatives and the most intensively-studied

38   non-human primate in the wild, chimpanzees have played a particularly important role in

39   the study of animal culture (Goodall 1973; McGrew 1992; Boesch 1996; Boesch and

40   Tomasello 1998). A landmark survey of geographic variation in chimpanzee behaviour

41   found 39 behaviours, including various forms of tool use, grooming, and courtship

42   behaviour, that were common in at least one chimpanzee group but absent in at least one

43   other, and for which an ecological explanation for this absence was judged to be unlikely,

44   (e.g., a lack of 'termite fishing' even though the appropriate termite species was present)

45   (Whiten *et al.* 1999; Whiten *et al.* 2001). This so-called "method of exclusion", which

46   infers the existence of culture by eliminating ecological explanations for the patterning of

47   between-group behavioural variation, has since been applied to several other primate and

48   non-primate species, and is now the dominant approach used to identify animal culture in

49   the wild (Rendell and Whitehead 2001; Hohmann and Fruth 2003; Perry *et al.* 2003; van

50   Schaik *et al.* 2003).

51   In a pattern reminiscent of between-group variation in human behaviour, each

52   chimpanzee group had its own unique combination of these putative cultural variants.

53   This complex, mosaic pattern of between-group variation in behaviour was very different

54   than that observed in prior studies of animal culture, where in most cases only one type of

55   behaviour varied among groups (e.g., bird song dialect (Marler and Tamura 1964)).

56   Despite various other species showing patterns of behavioural diversity that approach

57 levels shown in chimpanzees, for many, chimpanzees remain "the prime exemplar of

58 animal culture" (Boesch 2003; McGrew 2004; Laland *et al.* 2009).

59   Research conducted in captivity shows that chimpanzees have the requisite social

60 learning abilities to produce stable differences in group-specific behaviour (Whiten *et al.*

61 2005; Horner *et al.* 2006; Bonnie *et al.* 2007; Whiten *et al.* 2007; Price *et al.* 2009). In

62 one experiment (Whiten *et al.* 2005), for example, two chimpanzees were isolated from

63 their respective groups and trained in alternative techniques to use a tool to gain access to

64 food in an experimental apparatus. These two "demonstrators" were then re-introduced

65 into their original groups, whose behaviour was then compared with each other and with

66 that of a third group who had no such access to a trained demonstrator. Chimpanzees in

67 the first two groups predominately performed the technique of their demonstrator, while

68 chimpanzees in the third group did not learn to gain access to the food.

69   However, although the social learning abilities of chimpanzees are sufficient to

70 produce group differences in behaviour, this does not necessarily indicate that all or even

71 most of the behavioural variants observed in the wild arise as a result of social learning,

72 and thus represent true cultural variants (Galef 1990; Tomasello 1990; Boesch 1996;

73 Galef 2009; Laland *et al.* 2009). Some critics argue that insufficient attention has been

74 paid to the possibility that genetic differences are responsible for behavioural variation

75 between chimpanzee groups (Galef 1990; Heyes 1994; Heyes and Galef 1996; Laland *et*

76 *al.* 2006; Tennie *et al.* 2009). Recent research showing that individuals raised with no

77 opportunity to acquire the behaviour through social learning nevertheless exhibit

78 sophisticated abilities to use tools (crows) (Kenward *et al.* 2005) and process foods

79 (gorillas) (Tennie *et al.* 2008) suggests that complex behaviours can at least partly be

80   under genetic control, and thus that group differences in the underlying genetic

81   predispositions and abilities could plausibly contribute to group differences in behaviour.

82   Indeed, almost one-third of the putative cultural variants in the original report (Whiten *et*

83   *al.* 1999) of geographical variation in chimpanzee behaviour are found only in *Pan*

84   *troglodytes verus*, the most genetically divergent of the four chimpanzee subspecies, and

85   considered by some to represent a different species (Morin *et al.* 1994; Gagneux *et al.*

86   1999).

87   In the only systematic investigation of this issue, Lycett and colleagues (Lycett *et*

88   *al.* 2007; Lycett *et al.* in press) reasoned that if the patterning of intergroup variation in

89   behaviour is primarily the product of genetic differences between subspecies, then a tree

90   of the relationships between chimpanzee groups generated from a cladistic analysis of the

91   39 putative cultural variants should have more phylogenetic structure when two

92   subspecies are considered together than a tree generated from the East African subspecies

93   alone. They failed to find more phylogenetic structure in the two-subspecies than the

94   single-subspecies tree, and thus concluded that the patterning of between-group variation

95   in chimpanzee behaviour fit a cultural explanation better than a genetic one.

96   While an important first step towards an explicit investigation of the role of

97   genetic differentiation in generating intergroup variation in behaviour, this study has four

98   major limitations. First, as acknowledged by Lycett and colleagues (Lycett *et al.* in

99   press), at present there is no well-accepted statistical methodology for comparing the

100   extent of phylogenetic structure in two different trees. Second, recent simulation studies

101   show that measures of phylogenetic structure are very sensitive to rates of evolution

102   (Nunn *et al.* in press). Even if the behavioural variants were genetically determined, then

103 a sufficiently high rate of evolution, which could be caused by selection, could produce a

104 lower signal of phylogenetic structure in a tree with deeper phylogenetic separation

105 (Nunn *et al.* in press). Third, the one-subspecies versus two-subspecies analysis

106 presupposes that only genetic differentiation between subspecies, but not genetic

107 differentiation among groups within a single subspecies, can affect behavioural variation

108 among groups. Although the statement that "populations within East Africa cannot be

109 distinguished" (Lycett *et al.* 2007) p. 17589 is technically correct in the sense that there is

110 sharing of mitochondrial DNA (mtDNA) haplotypes across the subspecies range,

111 quantitative analyses show that there is as much geographical structuring of genetic

112 variation within the East African subspecies as within the entire human species (Goldberg

113 and Ruvolo 1997). That the extent of genetic differentiation among chimpanzee groups

114 belonging to the same subspecies is sufficient to affect between-group behavioural

115 variation is suggested by the finding that genetically influenced variation in body size is

116 implicated in differences between the qualities of vocalizations of two groups of

117 chimpanzees belonging to the same East African subspecies (Mitani *et al.* 1999). Finally,

118 the method employed by (Lycett *et al.* 2007; Lycett *et al.* in press) purports to test only

119 whether genetics can be excluded as a cause for *overall* levels of similarity in the

120 behavourial repertoires of chimpanzee groups; it offers no insight into how strongly the

121 distribution of each of the individual behavioural variants follows (or does not follow)

122 patterns of between-group genetic differentiation. Some authors have suggested that

123 differences in non-vocal communicative behaviours are particularly unlikely to result

124 from differences in underlying genetic predispositions, as this class of behaviours is less

125 likely than other classes of behaviour (e.g., tool-use in a foraging context) to be

126   influenced by the differential operation of natural selection according to local ecological

127   conditions (Boesch 1996; van Schaik 2009).

128   Here we take a more direct approach to the question of whether genetics can be

129   excluded as playing a role in generating intergroup variation in the behaviour of wild

130   chimpanzees by measuring levels of genetic differentiation among nine groups of wild

131   chimpanzees (three from the West African *P.t. verus* and six from the East African *P.t.*

132   *schweinfurthii* subspecies), and comparing these results with patterns of between-group

133   behavioural variation. Our study involved five steps. First, we sequenced most of the

134   members of each of the nine groups at the first hypervariable region of the maternally

135   inherited mtDNA and estimated levels of between-group genetic

136   similarity/differentiation. Second, we converted the behavioural data of the original study

137   of geographical variation in chimpanzee behaviour (Whiten *et al.* 1999) (as well as data

138   from two newly assessed chimpanzee groups) into numerical codes reflecting how

139   frequently each of the 39 behaviours occurred in each chimpanzee group. Third, we used

140   these behavioural data to generate, for each of the 36 pairs of groups, (1) a measure of the

141   overall level of behavioural similarity (*sensu* (Lycett *et al.* 2007; Lycett *et al.* in press)),

142   and (2) a measure of the level of differentiation for each of the individual behavioural

143   variants. Fourth, we examined how well patterns of between-group genetic variation

144   matched patterns of between-group (1) overall behavioural similarity and (2)

145   differentiation for each of the individual behavioural variants. And fifth, we tested

146   whether the pattern of between-group genetic differentiation predicted patterns of

147   between-group behavioural differentiation less well for behavioural variants involved in

148   non-vocal communication than it did for other types of behavioural variants.

149

Results and Discussion

151   We found that the overall level of genetic differentiation among the 9 groups was

152   substantial (AMOVA value = 0.49, p = 0.00001), and that the majority of pairs of groups

153   (28 / 36 = 77.8 %) were significantly genetically differentiated from one another (Table

154   1). Of the 12 pairs of groups showing no significant genetic differentiation, three were

155   located in the same block of continuous forest (Mahale K and M, Kibale Kanayawara and

156   Ngogo, Taï North and South), and four involved pairs that contained the poorly

157   genetically sampled Mahale K group.

158   When comparing the genetic and behavioural data, we found that levels of genetic

159   similarity and levels of overall behavioural similarity between chimpanzee groups were

160   strongly and significantly correlated (Pearson matrix permutation correlation, N = 26

161   pairs, R = 0.59, p = 0.001) (figure 1; table 1). The relationship between genetic similarity

162   and overall behavioural similarity was less strong and failed to reach statistical

163   significance when calculated for the much smaller data set of only the 6 groups belonging

164   to the East African subspecies (Pearson matrix permutation correlation, N = 15 pairs of

165   groups, R = 0.35, p = 0.18). These results suggest that genetic differentiation cannot be

166   excluded as an explanation for overall patterns of behavioural variation among

167   chimpanzees, and may even play a role in generating behavioural variation among groups

168   within a single subspecies.

169   The strong correlations between genetic and overall behavioural similarity,

170   however, do not necessarily preclude social learning as contributing to the patterning of

171   behavioural variation among chimpanzee groups. If emigrating females carry the

172   behavioural variants of their natal group to their new group, then groups that share more

173   migrants are likely to be more behaviourally similar. High migration rates between

174   groups could thus result in a positive correlation between genetic and behavioural

175   similarity, even if behavioural variants were completely socially learned. It is thus only

176   when patterns of behavioural and genetic similarity are discordant that inferences can be

177   made about the role of social learning in generating geographical variation in behaviour.

178   Our second goal was therefore to identify those behavioural variants whose

179   geographical distribution did not match the predictions of the genetic hypothesis,

180   suggesting they represent true socially learned cultural variants. We found that the

181   individual behavioural variants varied continuously in the extent to which their

182   distribution matched patterns of genetic differentiation (table 2). The combination of a

183   relatively modest sample size (N = 6 to 36 pairs of groups) and the stringent alpha level

184   (e.g., in this case, a Bonferroni correction of $0.05 / 24 = 0.002$) that is required to correct

185   for multiple comparisons means that there is very low power to reject the null hypothesis

186   that the distribution of each behavioural variant is predicted by genetic differentiation.

187   Thus, it is not possible to make strong inferences about which of the individual

188   behavioural variants can and which of the individual behavioural variants cannot be

189   excluded as being explained by patterns of genetic differentiation.

190   However, we did find that, as a whole, the distribution of non-vocal

191   communicative behavioural variants was less well predicted by patterns of genetic

192   differentiation than was the distribution of the other types of behavioural variants (table

193   2, figure 2). The mean of the Spearman rank correlation coefficients between behavioural

194   differentiation and genetic differentiation was significantly higher among the

195 communicative behavioural variants ($\overline{X}$ = 0.01, 95 % C.I. = 0.07) than among the non-

196 communicative behavioural variants ($\overline{X}$ = 0.22, 95 % C.I. = 0.11) (independent samples t

197 test; t (29.3) = 3.234, p = 0.003).

198

199 **Conclusions**

200   Here we have shown that genetic differences cannot be excluded as playing a

201 major role in structuring patterns of behavioural variation among chimpanzee groups,

202 particularly for behaviours not involved in non-vocal communication. As others have

203 noted, the method of exclusion may lead to an underestimation of the true number of

204 cultural variants that exist in the wild (Boesch 1996; Laland *et al.* 2006; Laland *et al.*

205 2009). Our results showing that chimpanzee groups separated by more than ≈ 300 km are

206 likely to show significant genetic differentiation suggests that if the method of exclusion

207 is strictly applied, then only behaviours that vary among chimpanzee groups that are very

208 geographically close should be considered as cultural variants (e.g. (Mobius *et al.* 2008)).

209 It has been proposed (Lefebvre 1995; Franz and Nunn 2009; Kendal *et al.* 2009) that

210 mathematical methods to identify a statistical 'signature' of transmission of a behavioural

211 variant through social learning are a promising way to investigate culture in the wild for

212 animals, like chimpanzees, where definitive translocation experiments (e.g. (Helfman and

213 Schultz 1984)) are impossible for logistic and ethical reasons. Unfortunately, while we

214 often have a good understanding of the distribution of a behaviour among the individuals

215 within a group, the diffusion processes that led to that distribution are rarely observed

216 (Perry *et al.* 2003). Comparing patterns of behavioural variation with patterns of kinship

217 among individuals within the same social group may be a more tractable way to

218 investigate animal culture in the wild (Krutzen *et al.* 2005), particularly in species like

219 chimpanzees where the relatively weak influence of kinship on patterns of affiliation

220 (Langergraber *et al.* 2007; Langergraber *et al.* 2009) means that evidence for social

221 learning (i.e., animals that interact with each other more frequently are more likely to

222 share the behavioural variant) is not confounded with evidence for genetic inheritance

223 (i.e., close relatives are more likely to share the behavioural variant). In sum, diverse

224 methodologies will be essential to resolving the long-standing debate of the relative

225 contributions of genetics, social learning, and other factors in generating geographical

226 variation in animal behaviour.

227

228 **Materials and Methods**

229

230 We examined mitochondrial (mtDNA) variation (354 bases of the first

231 hypervariable region) in nine groups of chimpanzees (numbers of adolescent and adult

232 individuals sequenced / number of adolescent and adult group members present at time of

233 sampling in brackets): the Bossou group (12/12) of Guinea, the North (8/11) and South

234 (16/26) groups of Taï National Park, Cote d'Ivoire, the Sonso group (28/28) of Budongo

235 Forest Reserve, Uganda, the Ngogo (89/89) and Kanyawara (20/20) groups of Kibale

236 National Park, Uganda, the M (32/32) and K (3/Unknown) groups of Mahale Mountains

237 National Park, Tanzania, and the Kasekela (38/38) group of Gombe Stream National

238 Park, Tanzania. mtDNA sequences for five of the groups were previously published:

239 Bossou (Shimada *et al.* 2009), Sonso (Langergraber *et al.* 2007), Gombe (Liu *et al.*

240 2008), Ngogo (Langergraber *et al.* 2007), Kanyawara (Langergraber *et al.* 2007). We

241 generated new mtDNA sequences for the Taï North and South groups, the Mahale M and

242 K groups, and the Gombe Kasekela group, following previously described procedures

243 [24, 25]. The Genbank (http://www.ncbi.nlm.nih.gov) accession numbers for the

244 chimpanzee mtDNA sequences used in this study are EU077270-EU077418,

245 XXXXXXXX-XXXXXXXX, and XXXXXXXX-XXXXXXXX.

246   AMOVA and pairwise F_{ST} values were calculated using Arlequin 3.1 (Excoffier *et*

247 *al.* 2005), with genetic distances between haplotypes measured using the number of

248 nucleotide differences, and statistical significance was assessed by comparison with

249 genetic differentiation calculated on random data sets where mtDNA haplotypes were

250 permuted among groups. Although mtDNA is unlikely to directly code for any of the

251 behavioural variants considered here, it is an excellent marker for determining overall

252 levels of genetic similarity among groups, particularly in species such as chimpanzees

253 where females rather than males move between groups. This is supported by the strong

254 correlation between mtDNA genetic distance and geographical distance among the nine

255 chimpanzee groups included in this study (Pearson correlation matrix permutation, $N =$

256 36 pairs of groups, $R = 0.96$, $p = 0.00005$).

257   For six of the chimpanzee groups in this study (Bossou, Sonso, Kanyara, Mahale

258 M and K, Kasekela), we used the behavioural codes as described in the original paper on

259 geographical variation in chimpanzee behaviour (Whiten *et al.* 1999; Whiten *et al.* 2001).

260 For Taï North we changed three codes from the original paper, as one of us (C.B., the

261 director of this field site) decided that these new codes were more accurate: 'Hand-clasp'

262 was changed from habitual to present, 'Knuckle-knock' was changed from customary to

263 habitual, and 'Branch-slap' was changed from customary to absent. We repeated our

264   analyses of the relationship between overall behavioural and genetic similarity using the

265   original codes for Taï North and found no qualitative changes in our results (Pearson

266   correlation matrix permutation, $N = 36$, $R = 0.61$, $p = 0.001$). Taï South group, newly

267   coded for this study by C.B., had the same codes as Taï North, with the following two

268   exceptions: 'Bee-probe' was coded as present and 'Marrow-pick' as habitual. Ngogo,

269   newly coded by J.M. and K.L. for this study, had the same codes as Kanyawara, with the

270   following two exceptions: 'Seat-vegetation' was coded as habitual, and 'Leaf-clip,

271   mouth' was coded as customary. The behavioural variant 'Branch-din' was excluded

272   from all analyses because it was absent in all nine of the chimpanzee groups included in

273   this study. Thus, our study examined only 38 of the 39 putative cultural variants

274   described in the original study on geographical variation in chimpanzee behaviour

275   (Whiten *et al.* 1999; Whiten *et al.* 2001). We made no attempt to include behaviours now

276   known or suspected to vary between chimpanzee groups that were not included in this

277   original study (e.g., 'social scratch' (Nishida *et al.* 2004)).

278   We converted the behavioural codes into numbers as follows: (3) 'customary', the

279   behaviour occurs in all or most able-bodied members of at least one age-sex class (such

280   as adult males); (2) 'habitual', the behaviour is not customary but has occurred repeatedly

281   in several individuals, consistent with some degree of social transmission; (1) 'present',

282   the behaviour is neither customary nor habitual but is clearly identified; (0) 'absent', the

283   behaviour has not been recorded and no ecological explanation is apparent; (?)

284   'ecological explanation', absence is explicable because of a local ecological feature; and

285   (?) 'unknown', the behaviour has not been recorded, but this may be due to inadequacy of

286   relevant observational opportunities. Our numerical coding system differs from that used

287 in the study of Lycett and colleagues (Lycett *et al.* 2007; Lycett *et al.* in press), in that

288 these authors did not distinguish between behavioural variants that were absent and those

289 that were absent due to an ecological reason, coding both types as 0.

290   We then used these data to calculate Pearson correlations between each of the 36

291 pairs of chimpanzee groups, giving a measure of overall behavioural similarity that could

292 potentially range from -1 to 1. We compared this matrix of overall behavioural similarity

293 to the matrix of genetic similarity ($1 - F_{ST}$) using a Pearson matrix correlation test. For the

294 analysis of the relationship between genetic differentiation and the distribution of the

295 individual behavioural variants, we created a matrix consisting of the absolute value of

296 the difference in the numerical code between each of the communities, such that

297 communities that were similar for the behavioural variant had a score of 0 (i.e., both had

298 the same code), and communities that were very different for the behavioural variant had

299 a score of 3 (i.e., 'habitual' in one group and 'absent' in the other). We then calculated a

300 Spearman rank correlation matrix permutation test between each of these 38 matrices and

301 a matrix of genetic differentiation (F_{ST}). The independent samples t-test we used to

302 compare the average of the Spearman rank correlations between behavioural

303 differentiation and genetic differentiation of the communicative and non-communicative

304 behaviours accounted for unequal variances between these two groups (Levene's test for

305 equality of variance, $F = 5.159$, $p = 0.03$). This independent samples t-test was computed

306 on the 34 behavioural variants where at least 15 pairs of groups did not have a missing

307 value (i.e., 'ecological explanation' or 'unknown').

308   All matrix permutation tests used 10,000 permutations.

309

317

318   **Table and Figure Captions**

319

320   Figure 1. The relationship between levels of overall behavioural similarity and levels of

321   genetic similarity in 36 pairs of wild chimpanzee groups.

322

323   Table 1. Genetic similarity (below diagonal) and overall behavioural similarity (above

324   diagonal) in 36 pairs of chimpanzee groups. Pairs where genetic differentiation is

325   statistically significantly different from 0 are in listed in bold.

326

327   Table 2. Spearman rank correlations between behavioural distance and genetic distance

328   for the individual behavioural variants. Also shown are the classifications of behavioural

329   variants as non-vocal communicative or not. Behavioural variants are listed in descending

330   order of strength of negative correlation with genetic distance.

331

332 Figure 2. Mean of the correlation coefficients between genetic and behavioural

333 differentiation for non-vocal communicative and other types of behavioural variants.

334 Error bars represent 95 % confidence intervals.

335

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475   Table 1

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	Bossou	Taï North	Taï South	Kibale Ngogo	Kibale Kanyawara	Budongo Sonso	Gombe Kasekela	Mahale K	Mahale M
Bossou		-0.02	0.03	-0.10	-0.16	0.24	-0.19	-0.16	0.22
Taï North	0.98		0.96	0.02	-0.04	-0.11	-0.08	-0.02	-0.14
Taï South	0.99	1.06		0.11	0.05	-0.05	-0.01	-0.02	-0.08
Kibale Ngogo	**0.29**	**0.28**	**0.29**		0.98	0.23	0.10	0.36	0.40
Kibale Kanyawara	**0.31**	**0.29**	**0.32**	0.98		0.20	0.18	0.35	0.41
Budongo Sonso	**0.26**	**0.24**	**0.28**	**0.90**	**0.85**		-0.20	-0.02	0.19
Gombe Kasekela	**0.32**	**0.30**	**0.32**	**0.89**	**0.85**	**0.88**		0.12	0.13
Mahale K	**0.44**	**0.45**	**0.44**	0.94	0.84	**0.77**	0.93		0.58
Mahale M	**0.24**	**0.22**	**0.26**	**0.77**	**0.65**	**0.63**	**0.75**	1.18	

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480   Table 2

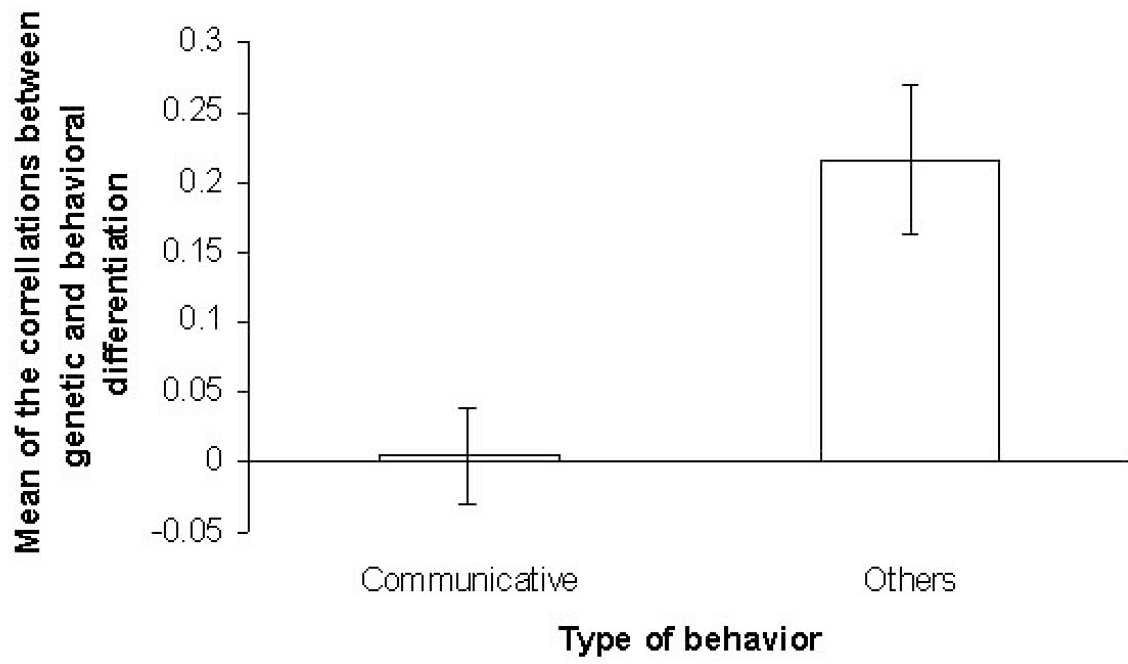| behavioral variant	N	spearman's r	p	non-vocal communicative?
Leaf-squash (squash ecto-parasite on leaf)	28	-0.21	0.26	no
Self-tickle (tickle self using objects)	36	-0.14	0.56	no
Leaf-clip, fingers (rip single leaf with fingers)	36	-0.11	0.48	yes
Leaf-clip, mouth (rip parts off leaf, with mouth)	36	-0.09	0.61	yes
Ant-dip-wipe (manually wipe ants off wand)	36	-0.07	0.63	no
Leaf-inspect (inspect ecto-parasite on hand)	28	-0.03	0.89	no
Leaf-dab (leaf dabbed on wound, examined)	36	-0.03	0.82	no
Leaf-strip (rip leaves off stem, as threat)	36	-0.02	0.88	yes
Fly-whisk (leafy stick used to fan flies)	21	0.00	0.99	no
Food-pound onto other (e.g., stone)	21	0.00	0.99	no
Stem pull-through (pull stems noisily)	36	0.00	0.99	yes
Expel/stir stick expels or stirs insects)	21	0.02	0.93	no
Branch-slap (slap branch, for attention)	36	0.03	0.82	yes
Ant-fish (probe used to extract ants)	36	0.03	0.78	no
Aimed-throw (throw object directionally)	36	0.06	0.60	no
Shrub-bend (squash stems underfoot)	36	0.07	0.63	yes
Lever open (stick used to enlarge entrance)	36	0.10	0.58	no
Fluid-dip (use of probe to extract fluids)	36	0.14	0.31	no
Bee-probe (disable bees, flick with probe)	36	0.15	0.35	no
Knuckle-knock (knock to attract attention)	36	0.16	0.28	yes
Hand-clasp (clasp arms overhead, groom)	36	0.18	0.20	no
Club (strike forcefully with stick)	36	0.24	0.10	no
Leaf-napkin (leaves used to clean body)	36	0.25	0.10	no
Nut-hammer, wood hammer on stone anvil	15	0.28	0.24	no
Nut-hammer, other (e.g., on ground)	15	0.28	0.24	no
Food-pound onto wood (smash food)	21	0.35	0.07	no
Index-hit (squash ecto-parasite on arm)	36	0.35	0.05	no
Marrow-pick (pick bone marrow out)	36	0.39	0.04	no
Rain dance (slow display at start of rain)	36	0.39	0.03	no
Seat-vegetation (large leaves as set)	36	0.49	0.02	no
Leaf-groom (intense 'grooming' of leaves)	36	0.72	0.01	no
Ant-dip-single (one handed dip stick on ants)	36	0.84	0.00	no
Nut-hammer, stone hammer on stone anvil	15	0.85	0.02	no

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482   Figure 1.

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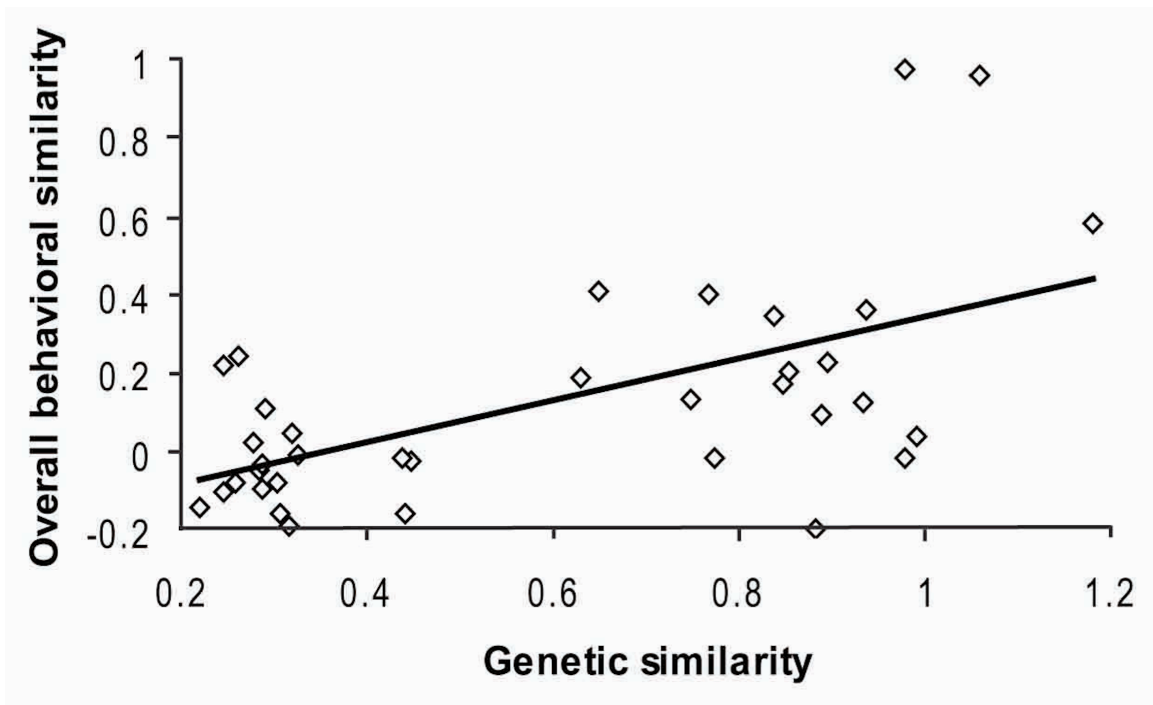
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486   Figure 2

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