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Invited reply

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In our original paper [1], we found that overall levels of genetic and behavioural dissimilarity between chimpanzee groups are highly and statistically significantly correlated, and that only a small number of behaviours vary between genetically similar groups. Our main conclusion from these results was that genetic differences between chimpanzee groups cannot be excluded from generating differences in their behaviour, and thus that caution should be drawn in attributing such differences to ‘culture’. This contradicted the earlier work of Lycett *et al.* [2,3], who had reached the opposite conclusion based on phylogenetic analyses of chimpanzee behavioural variation.

In their comment on our original paper [1], Lycett *et al.* [4] state that we claimed that their failure to analyse the behaviours individually is a reason to reject their findings. This appears to be a misreading of our paper, as we made no such claim. We simply stated that Lycett *et al.*'s method ‘furnishes no insight into how strongly the distribution of each of the individual behavioural variants follows or fails to follow patterns of between-group genetic dissimilarity’ [1, p. 409]. We agree with Lycett *et al.* [4] that analysing individual behaviours is a potentially informative approach, and it was precisely for this reason that we conducted such analyses. The failure of Lycett *et al.* to analyse behavioural variation at the individual level is a limitation of their work only in the sense that an analysis solely at the overall level potentially provides less insight than a combination of overall and individual level analyses.

Rather, our actual criticisms of Lycett *et al.*'s previous work pertain to the fundamental assumptions of their approach. Lycett *et al.* [4, p. 1] argue that ‘[p]hylogenetic analyses of chimpanzee genetic data have consistently yielded results suggesting that if the genetic hypothesis is to be supported, behavioural data should exhibit *decreased* phylogenetic structure when data from a single subspecies are analysed as opposed to when two subspecies are analysed’. As they failed to find more phylogenetic structure in the most parsimonious cladogram of a two-subspecies than a one-subspecies analysis, they concluded that genetic differences between chimpanzee groups can be excluded as playing a role in their behavioural variation.

We find it unwarranted to draw such a strong conclusion from a negative result, as there are several possible explanations for a failure to find greater phylogenetic structure in a two- than one-subspecies cladogram, even

if the behavioural variants are genetically inherited. Note that ‘while the most parsimonious cladogram does represent the best summary of the data to hand and is thus the preferred hypothesis of relationships among the study taxa, it is naive to assume that it also represents the “true phylogeny”’ [5, p. 198]. The main difficulty in reconstructing phylogenetic relationships comes from distinguishing variants shared owing to recent common ancestry from variants shared for other reasons (homoplasies). Several studies of the phylogenetic relationships among extant species, including one by Collard & Wood [6], second author on the aforementioned studies [2,3], have shown that morphological characters can show such high levels of homoplasy that even strongly supported estimates of phylogeny can differ greatly from those that are well-known and accepted from genetic data. Particularly for closely related taxa such as the chimpanzee groups considered here, there are two factors that hamper the use of genetically inherited behavioural variants to meaningfully reconstruct the groups’ phylogeny in terms of a bifurcating tree process. The first is that the accuracy of phylogenetic reconstruction is strongly influenced by the number of sampled taxa [7]; unfortunately, Lycett *et al.*'s cladograms were necessarily constructed from only seven of the thousands of chimpanzee groups extant in Africa. The second is that these seven chimpanzee groups have experienced varying amounts of recent and contemporary gene flow among themselves, a process which has a strong impact on the ability to accurately reconstruct phylogenies, even when these are constructed using large genetic datasets [8]. It is for these and other reasons that biologists typically employ the sorts of phylogenetic methods applied by Lycett *et al.* only when attempting to reconstruct the evolutionary relationships of taxa that are separated at the species level or above [5].

Thus, not only is there reason to be cautious in drawing strong conclusions from Lycett *et al.*'s negative results regarding greater phylogenetic structure in the two-subspecies than the one-subspecies tree, there are also reasons to doubt whether, even if the behavioural variants were completely genetically inherited, we could ever reasonably expect that the cladograms compared by Lycett *et al.* were the correct ones in the first place. Indeed, Lycett *et al.*'s most parsimonious cladogram in their two-subspecies analysis actually shows a near perfect match with geographical distances (and thus, as we showed in our paper, with genetics distances as well), with only one group (Budongo) grouping with the ‘wrong’ subspecies according to Lycett *et al.*'s interpretation of the predictions

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of the genetic hypothesis. More importantly, however, this most parsimonious cladogram is only slightly more so than the next best supported cladogram, in which Budongo 'correctly' groups with the other groups of the same subspecies.

We now turn to Lycett *et al.*'s [4] criticisms of our paper. We are in complete agreement with Lycett *et al.*'s [4, p. 2] statement that '... the method Langergraber *et al.* employed in their primary analysis can only distinguish between the genetic hypothesis and the culture hypothesis if genetic and behavioural dissimilarity are uncorrelated'. We do not understand, however, why Lycett *et al.* consider this a criticism of our work, as we already made this exact point in our paper [1, p. 411]: 'High migration rates between groups could thus result in a positive correlation between genetic and behavioural dissimilarity, even if behavioural variants were entirely socially learned. Thus, it is only when patterns of behavioural and genetic dissimilarity are *discordant* that inferences can be made about the role of social learning in generating geographical variation in behaviour'. Here, we would simply add that the suggestion that chimpanzee groups which experience high levels of female migration are likely to be behaviourally similar is an assumption that is in need of further testing; the only systematic study that has addressed this topic, conducted in vervet monkeys, showed that individuals selectively model their behaviour on individuals of the philopatric sex, raising questions about the ability of migrants to influence the behaviour of their new group [9].

While we also agree with Lycett *et al.* [4, p. 2] that the 'appropriate conclusion to draw is that the results of the analysis are inconclusive [with regards to genetics and/or culture influencing the patterning of between-group variation] due to methodological limitations', we are puzzled as to why they go on to argue that it is nevertheless inappropriate for us to conclude that a strong, positive correlation between behavioural and genetic dissimilarity indicates that we cannot exclude genetic dissimilarity as a potential cause of behavioural differences among chimpanzee groups. This line of reasoning is all the more strange considering that Lycett *et al.* [2, p. 17 589] themselves state that '... a correlation between geographical distance [and behavioural distance] does not exclude the possibility that the behaviours are genetically determined...' Why is it appropriate to conclude that genetic distance cannot be excluded as a potential cause of behavioural variation if it is correlated with *geographical* distance, but inappropriate to conclude that genetic distance cannot be excluded as a potential cause of behavioural variation if it is correlated with *genetic* distance?

Lycett *et al.* [4] apply similar reasoning in their criticism of our secondary analyses, where we examined the relationship between genetic dissimilarity and the distribution of the individual behavioural variants. As we noted in our original paper, one of the major reasons for conducting the first two of these secondary analyses

of the individual behavioural variants is precisely because it is only when patterns of genetic and behavioural dissimilarity are discordant that we can make inferences about the processes (genetic or cultural) responsible for between-group variation in behaviour. We would thus agree with Lycett *et al.* that the first two of our three secondary analyses show that we *can* exclude the genetic explanation for several behaviours (13.2–52.6%, depending on what one considers to be genetically similar groups). However, this still leaves many behaviours for which we *cannot* exclude the genetic hypothesis, further justifying our conclusion that genetic differences cannot be excluded as playing a major role in group differences in chimpanzee behaviour.

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