Derex *et al.* reply

REPLYING TO C. Andersson & D. Read *Nature* **511,** http://dx.doi.org/10.1038/nature13411 (2014)

In the accompanying Comment[1], Andersson & Read challenge our results[2] that group size influences cultural complexity. Using a dual-task computer game, our experiment demonstrated that an increasing group size prevents the loss of cultural traits (simple and complex), promotes their improvements and prevents cultural richness to disappear[2]. Among these various effects, Andersson & Read[1] are questioning the finding that larger groups favour the persistence of the complex trait.

Andersson & Read[1] claim that the expected number of groups that only exploit the simple task is more than expected if individuals in larger groups were behaving as individuals in smaller groups. Thus, they conclude that group size negatively affects the individual ability to exploit the complex task. Instead our data show the opposite pattern: individuals in larger groups tend to be more able to exploit the complex task (Fig. 1), thus supporting the group size hypothesis.

The first issue with the analysis of Andersson & Read[1] is their estimation of the individual probability to exploit the simple task. Indeed, their method is expected to provide a correct estimation only if individuals behave independently of their other group members. As they claim that individuals' ability is affected by group size, this is quite problematic.

The expected number of groups exploiting only arrowheads should be computed from the probability that a single, isolated individual exploits the simple task. This probability is not available in our data, as individuals were always part of a group. To get around this, we used a generalized linear model on individual data to estimate this probability. We obtained a probability ($P = 0.80$) that a single individual exploits the simple task on the last step of the experiment. Using this probability, we computed the probability of getting outcomes as extreme as, or more extreme than, our observed data for each group size: $\Pr(X_2 \geq 8) = 0.873$; $\Pr(X_4 \geq 5) = 0.595$; $\Pr(X_8 \geq 2) = 0.629$ and $\Pr(X_{16} \geq 1) = 0.295$. Thus, for each group size, the expected number of groups that do not exploit the complex task is not significantly different from expected. We then combine P values using Fisher's method[3], and obtain an overall P value of 0.79.

Our initial analysis[2] showed that the probability of maintaining the complex trait within a group is positively affected by group size. Even if explained by sample size effect, this supports the group size hypothesis: sample size effect is expected to be the main mechanism by which group size affects cultural evolution[4–6]. Sample size effect should promote cultural evolution, unless the individual probabilities to exploit the task decrease drastically with group size. Here our data suggest that the individual probability of exploiting the simple task increases with group size (Fig. 1). In sum, analyses at group and individual levels support the group size hypothesis and are consistent with results from other recent experimental studies[7,8].

Culture is a group process that arises as a result of underlying individual-level mechanisms[9,10]. In order to study cultural evolution, two levels of analysis are therefore workable. The analysis of Andersson & Read[1] illustrates that individuals' behaviours can hardly be deduced from groups behaviours. Thus, each level of analysis can provide specific information. Depending on the question, analyses should be conducted at one level, or both, but conclusions should always be drawn accordingly.

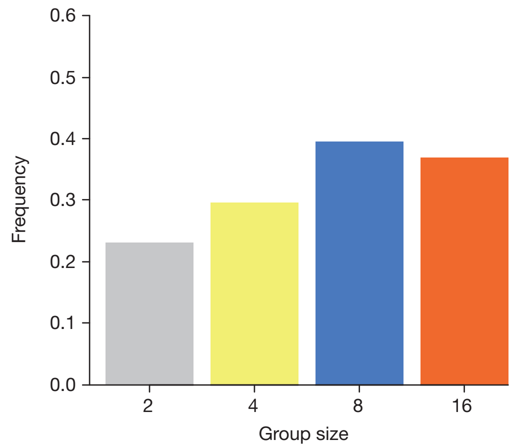

Figure 1 | Frequency of individuals exploiting the complex task according to group size. Group size had a positive and non-significant effect on the individual probability to exploit the complex task (linear: $\chi^2 = 2.53$, d.f. = 1, $P = 0.11$; quadratic: $\chi^2 = 2.15$, d.f. = 1, $P = 0.14$). Older players tend to be less likely to exploit the complex task ($\chi^2 = 3.47$, d.f. = 1, $P = 0.06$). Players who 'died' during the game[2] were excluded from the analysis (2-player groups: $n = 26$; 4-player groups: $n = 44$; 8-player groups: $n = 86$; 16-player groups: $n = 174$).

Maxime Derex[1], Marie-Pauline Beugin[1], Bernard Godelle[1] & Michel Raymond[1,2]
[1]University of Montpellier II, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France.
email: maxime.derex@gmail.com
[2]CNRS, Institute of Evolutionary Sciences, CC 065, Place Eugène Bataillon, Montpellier 34095, France.

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