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Comment on "Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions"

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The claims of Danchin *et al.* (Research Articles, 30 November 2018, p. 1025) regarding long-lasting mate preference based on conformity may result from systematic experimental error. Even if mate copying were a genuine phenomenon, it is unlikely to result in persisting culture in the wild.

Danchin *et al.* (*1*) report long-lasting cultural transmission in *Drosophila melanogaster*. Their claims rest on the observation that females prefer to copulate with males resembling other males they have observed mating. We find that the authors' data deviate from the predictions of binomial statistics in ways suggestive of a latent and consistent bias across samples.

From a binomial model matching the mean effect size (with a probability of sharing the demonstrator's choice of 0.68) and a typical experiment size (63 flies), one expects a distribution of *P* values like the curves shown in black in Fig. 1A. The authors' data reject the null model (no mate copying) (i) more frequently than expected (they had an 89% chance to conclude a false negative at least once in the study) and (ii) with a distribution clustered more closely to the usual threshold for accepting a result ($P = 0.05$; Fig. 1A, blue line) than expected (mean in pink), as measured by the Kolmogorov-Smirnov (KS) test. These analyses hold for similar sample sizes and effect sizes.

The magnitude of the mate choice effect is also more consistent than would be expected by chance. When comparing populations that exhibit the same mate preference tendency, the resultant *P* values should be uniformly distributed between 0 and 1. The experimental *P* values, however, are skewed strongly toward 1, indicating far lower variance in preference than would be expected from an unbiased set of experiments (*P* value = 0.0051 compared to a uniform distribution; Fig. 1B, KS test).

A separate set of experiments [figure 6 in (*1*)] was carried out to study social transmission (transmission chains). The authors compare their experimental data to the predictions of the binomial model, finding an extremely close adherence, despite their low original sample size of 36 chains. We find that this adherence is actually implausibly close, matching the mean predictions of the binomial model more closely than almost all simulated experiments drawn from the actual model ($P = 0.07$, maximum absolute difference from the mean; Fig. 1C). Although the authors correctly note that their data are inconsistent with a model in which mate choice is unbiased, their data are also unlikely to arise from processes internal to the female and independent from the results of other experiments.

Our attempts to replicate mate copying were complicated by the fact that the coloring used by the authors to mark the males precludes courtship until sufficiently groomed away over tens of minutes to hours (*2*). We argue that inconsistent male coloring may be one source of bias, leading to more courting (and therefore copulation) of one color across demonstration and testing phases. Another source of bias may arise from the fact that the only functional criterion for knowing whether enough color remains after grooming is the mate-copying phenomenon itself. The authors note a strongly significant effect of experimenter ID on mate copying, pointing to methodological inconsistencies (*1*).

Independent of the statistical irregularities and methodological issues, persistent mate copying as reported here would be unlikely to exist in the wild. The authors note a pronounced effect of atmospheric pressure on social learning in *Drosophila* in their work here (*1*) and elsewhere (*3*). This is potentially crippling for the retention of culture through conformity: If the chain of transmission is broken, the history (culture) is essentially erased. The authors' simulations of cultural transmission do not incorporate this apparently important consideration. We used the authors' previously published data to estimate the effects of atmospheric pressure on social learning. This model was used to predict how daily fluctuations in atmospheric pressure would affect cultural transmission in realistic conditions. As shown in Fig. 2A, atmospheric conditions that alter social learning are frequent, which suggests that pressure must be taken into account. To do so, we repeated the authors' cultural longevity simulations, with the addition of daily variation of atmospheric pressure consistent with that observed in Blagnac and a modification of social learning that resem-

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bled the data presented by the authors (Fig. 2B). This modification shortened the maximum number of transmission steps (and the average length of a chain) by orders of magnitude at the largest population sizes (where the original analysis argued for extremely consistent culture) (Fig. 2, C and D). Even a temporary deviation from perfect conditions would erase any accumulated "culture." As most other results in this manuscript closely resemble data published elsewhere by the authors (*2*, *4*, *5*), this disputed finding is a foundation of the work in question.

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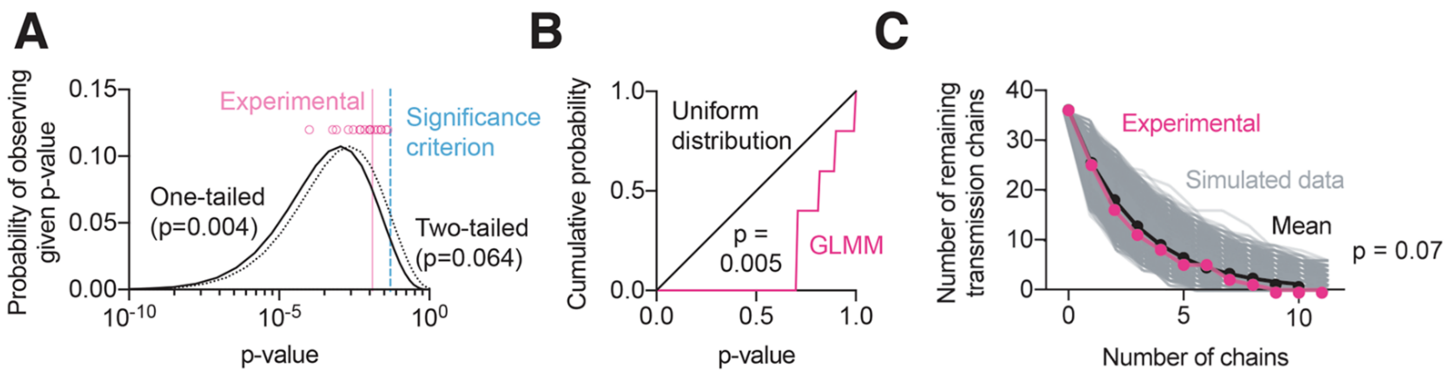

Fig. 1. Reported mate copying is unlikely to result from social learning. (**A**) The proportions of Danchin *et al*. do not adhere to binomial statistics, which suggests that population mate preference does not arise from independent trials. The data also closely hug the significance threshold of 0.05, often indicative of latent contaminating factors (*6*). Solid line, one-tailed binomial test; dotted line, two-tailed binomial test. (**B**) Danchin *et al*.'s generalized linear mixed model (GLMM) analysis of mate preference generates *P* values close to 1, indicating that the data are far less variable within graphs than would be expected by the generating distribution. (**C**) Transmission chains more closely resemble the mean of a binomial model than would be expected by chance, suggestive of a systematic effect on mate choice.

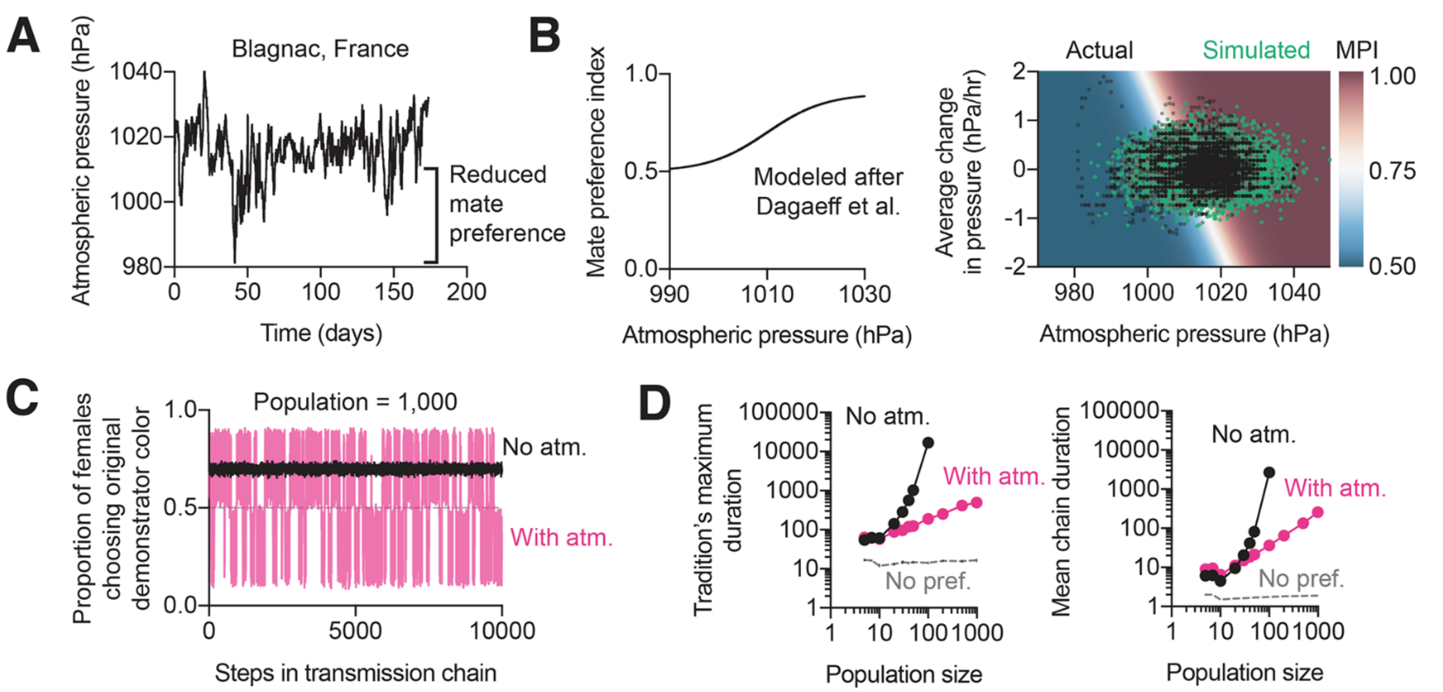

Fig. 2. *Drosophila* are unlikely to develop mate preference culture in the wild. (**A**) Air pressure measured at Toulouse-Blagnac airport every 30 min (*7*) frequently falls within the range known to affect social learning (*3*). (**B**) Left: Marginal effect of atmospheric pressure on mate preference index (MPI) in our model for zero average change in pressure. Right: Atmospheric pressure and rate of change in pressure at Toulouse-Blagnac airport (black) and simulated data drawn from a multivariate Gaussian used in our model (green) overlaid on those atmospheric conditions' effects on mate preference (blue-red gradient). (**C**) Example trace of the effects of atmospheric conditions on cultural longevity in a population of size 1000. The inclusion of atmospheric pressure markedly reduces the stability of the simulated culture. (**D**) Atmospheric pressure markedly reduces the duration of both the longest cultural traditions (left) and the average tradition (right).

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