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ANIMAL CULTURE

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

Etienne Danchin^{1*}†, Sabine Nöbel^{1,2*}, Arnaud Pocheville^{3*}, Anne-Cecile Dagaëff¹, Léa Demay¹, Mathilde Alphand¹, Sarah Ranty-Roby¹, Lara van Renssen^{1,4}, Magdalena Monier¹, Eva Gazagne⁵, Mélanie Allain^{1,6}, Guillaume Isabel⁶

Despite theoretical justification for the evolution of animal culture, empirical evidence for it beyond mammals and birds remains scant, and we still know little about the process of cultural inheritance. In this study, we propose a mechanism-driven definition of animal culture and test it in the fruitfly. We found that fruitflies have five cognitive capacities that enable them to transmit mating preferences culturally across generations, potentially fostering persistent traditions (the main marker of culture) in mating preference. A transmission chain experiment validates a model of the emergence of local traditions, indicating that such social transmission may lead initially neutral traits to become adaptive, hence strongly selecting for copying and conformity. Although this situation was suggested decades ago, it previously had little empirical support.

Researchers increasingly acknowledge that cultural traditions exist in nonhuman animals, including chimpanzees (1), orangutans (2), cetaceans (3), meerkats (4), and birds (5). However, thus far, examples have been limited to higher vertebrates. Exploration of this question in other taxa requires a transferable definition of culture. The typical criterion of culture is generally that transferred traits must be socially acquired and spread to others repeatedly (6).

Here, we propose a definition focusing on the properties of social learning. Integrating with previous studies, we define animal culture as phenotypic variation that is inherited through a form of social learning (i.e., learning from others) (criterion 1) (1, 5–9). Cultural inheritance will occur if social learning occurs across age classes (minimally, from older to younger individuals) (criterion 2) (9, 10), is maintained over the long term to be copied (criterion 3) (11), produces trait-based copying (criterion 4) (12), and incorporates repair or reinforcement mechanisms (13) [e.g., conformity (5, 14, 15) or information digitalization (16)] (criterion 5). Lastly, to connect this mechanistic definition with classical definitions focusing on the sole

existence of behavioral variation across populations, we tested whether the observed cognitive properties can generate local traditions spanning over generations (the most notable marker of culture) (13, 17). Cultural inheritance then makes cultural variation subject to selection and evolution.

We tested this multicriterion definition in fruitflies, which are known to have the capacity to socially learn sexual preferences from the observation of copulating conspecifics (18–20).

To test criterion 1 of social learning, we used the “speed-learning” design (Fig. 1) (20), testing whether, after watching a single demonstrator female choosing between two males of contrasting phenotypes, an observer female shows a bias for the male of the phenotype she saw being chosen during the demonstration. This two-step protocol involves a demonstration in a tube device (fig. S1) during which an observer female separated by a glass partition can watch a demonstrator female freely choosing between

one green and one pink male, immediately followed by a mate-choice test during which the observer female chooses to copulate with one of two new males, one of each color. The partition was transparent glass (informed females) or opaque white paper (uninformed control females).

The social learning index quantifying the learned bias toward the male of the color preferred during demonstrations (see S1.4 in the supplementary materials) differed between informed and uninformed replicates [generalized linear mixed model (GLMM), Wald χ^2 test; $n = 127$; $\chi^2_1 = 5.115$; $P = 0.024$] (Fig. 1B). Uninformed observer females chose in a way that did not differ from random (binomial test; $n = 63$; $P = 1$). Informed females mated preferentially with new males of the color they saw being chosen during the demonstration (binomial test; $n = 64$; $P = 0.002$) (Fig. 1B) whatever the color chosen during the demonstration (GLMM, Wald χ^2 test; $n = 127$; $\chi^2_1 = 0.0112$; $P = 0.916$). Thus, observer females learned to prefer the male of the color that was favored during demonstrations, exhibiting social learning and fulfilling criterion 1.

To satisfy criterion 2 of transmission across age classes, socially learned traits must be transmitted vertically or simply from older to younger individuals (9, 10). We replicated in tubes the horizontal informed treatment of criterion 1 (in which both females were 3 days old) as a positive horizontal control and compared it with an across-age-class treatment in which demonstrator females were 11 days older (i.e., of an age similar to that of the flies’ parents) (Fig. 2).

Both treatments were biased in favor of the male of the color that copulated during demonstrations (binomial tests; $n = 65$, $P = 0.025$, and $n = 63$, $P = 0.011$ for horizontal and across-age-class treatments, respectively) (Fig. 2). We found no difference between horizontal and across-age-class trials (GLMM, Wald χ^2 test; $n = 128$; $\chi^2_1 = 0.0555$; $P = 0.814$), showing that social transmission was equally efficient in the two contexts and thus fulfilling criterion 2.

To satisfy culture criterion 3, that of durability, learned preferences must be maintained

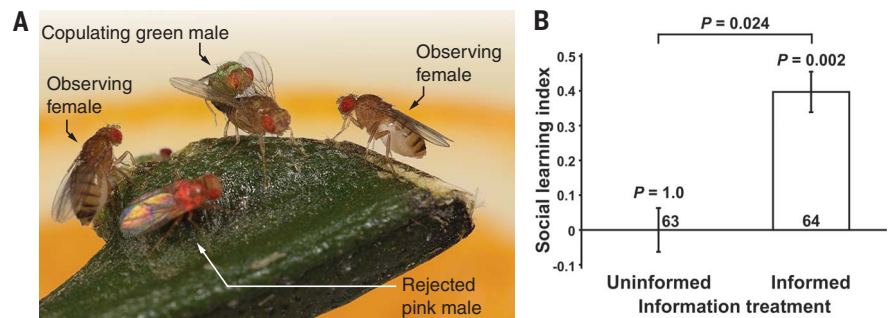


Fig. 1. Criterion 1 of social learning. (A) A situation of mate-copying in which two females watch a copulating green male while a pink male is rejected. (B) Social learning index of informed versus uninformed observer females. Positive social learning indices reveal preference for the male color chosen during demonstrations, whereas zero reveals random choice. P values above bars, binomial tests of departure from random choice; error bars, SEM.

¹Laboratoire Évolution and Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, IRD, 118 route de Narbonne, Bat 4R1, F-31062 Toulouse cedex 9, France.

²Université Toulouse 1 Capitole and Institute for Advanced Study in Toulouse (IAST), Toulouse, France. ³Department of Philosophy and Charles Perkins Centre, University of Sydney, Sydney, NSW 2006, Australia. ⁴Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, 9747 AG Groningen, Netherlands. ⁵Behavioural Biology Unit, Department of Biology, Ecology and Evolution, University of Liège, 4020 Liège, Belgium. ⁶Centre de Recherches sur la Cognition Animale, Centre de Biologie Intégrative, Université de Toulouse, CNRS, UPS, 118 route de Narbonne, F-31062 Toulouse cedex 9, France.

*These authors contributed equally to this work.

†Corresponding author. Email: etienne.danchin@univ-tlse3.fr

(11). Multiple spaced training (a series of training phases separated by resting periods) (21) in invertebrates and vertebrates leads to a stable form of long-lasting memory (22). We transposed this long-term memory protocol in *Drosophila* (23) to our visual social learning. After watching five conditioning demonstrations spaced by 15- to 30-min resting periods, observer females were tested for social long-term memory 24 hours later.

Informed spaced-trained flies displayed unusually high mate-copying after 24 hours (binomial test; $n = 62$; $P < 0.0001$) (Fig. 3A), but the uninformed ones did not (binomial test; $n = 65$; $P = 0.457$) (Fig. 3A). To confirm that this social long-term memory depends on de novo protein synthesis, a third group of spaced-trained flies fed an inhibitor of protein synthesis (cycloheximide) was tested in parallel. The cycloheximide treatment disrupted social long-term memory [$n = 65$, $P = 0.804$ (binomial test); $n = 192$, $\chi^2_1 = 15.6934$, $P = 0.0004$ (GLMM for the three treatment groups tested after 24 hours, Wald χ^2 test)] (Fig. 3A). Furthermore, cycloheximide-treated observer females tested shortly after a single demonstration did not differ from the horizontal control for criterion 2 [GLMM for informed cycloheximide-treated females versus non-cycloheximide-treated females of the horizontal control (Fig. 2); $n = 131$; $\chi^2_1 = 0.016$; $P = 0.898$ (Fig. 3B)] and showed significant mate-copying (binomial test; $n = 66$; $P = 0.036$) (Fig. 3B). Thus, the cycloheximide treatment did not impair mate-copying (21, 23). In a complementary experiment, we found that the high average learning index 24 hours after a spaced training (0.55, corresponding to a mate-copying index of 0.78) was produced by both spaced training and the 24-hour delay (see fig. S2). Thus, flies built de novo protein synthesis-dependent durable memory, meeting criterion 3.

Criterion 4 states that copying must be trait based (11, 12). In all the experiments described above [and most previous experiments (18, 20, 24, 25)], mate-choice tests used new green and pink males, suggesting that observer females learned to prefer any male of the same color. However, observer females may have confounded test males with demonstration males of the same color. To test whether females learned to prefer males of a given color, we used very different looking mutant males during mate-choice tests to rule out the possibility that observer females confounded test males with demonstrator males. Demonstrations involved a wild-type demonstrator female freely choosing between one green and one pink wild-type male, whereas males (green and pink) used in mate-choice tests were either both wild type (controls) or both curly-winged or white-eyed mutants (two experimental treatments). In a previous study, we showed that flies exhibit mate-copying with wild-type and curly-winged males instead of color variants, demonstrating that the flies do distinguish these genetic variants (26).

In all three treatments, during the mate-choice test observer females preferred males of the same color as the one chosen during demon-

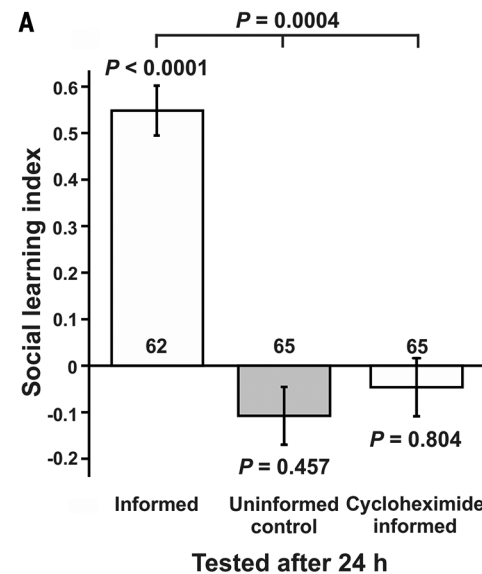
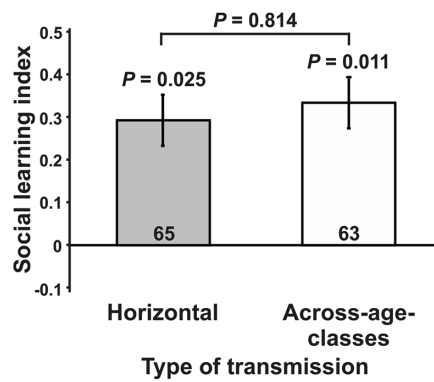
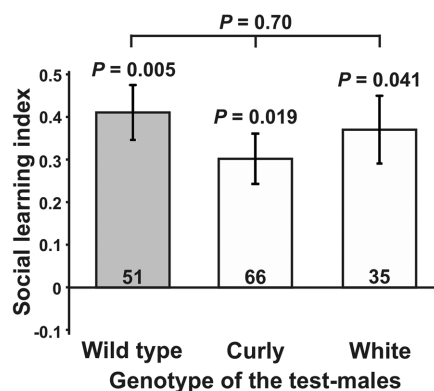


Fig. 3. Criterion 3 of durable social learning. (A) Long-term memory in mate-copying 24 hours after demonstrations. (B) Cycloheximide-treated females within the usual protocol of a single live demonstration immediately followed by the mate-choice test showed mate-copying similar to that of the non-cycloheximide-treated females of the horizontal-transmission group in Fig. 2. *P* values above bars, binomial tests of departure from random choice; error bars, SEM.



strations, with similar social learning indices (GLMM, genotype effect; $n = 152$; $\chi^2_2 = 0.714$; $P = 0.70$) (Fig. 4), despite their contrasting and distinguishable (26) genotypes relative to those of demonstrator males. Females performed trait-based copying, therefore meeting criterion 4.

Fig. 2. Criterion 2 of across-age-class transmission. Social learning indices of 3-day-old observer females learning from 3-day-old (horizontal) or 14-day-old (across-age-class) demonstrator females. *P* values above bars, binomial tests of departure from random choice; error bars, SEM.

Fig. 4. Criterion 4 of trait-based copying. Social learning indices according to the genotype of the males used during mate-choice tests. Demonstrations involved a wild-type demonstrator female freely choosing between one green and one pink wild-type male. We previously showed that females clearly distinguish wild-type from curly-winged genetic variants (26). *P* values above bars, binomial tests of departure from random choice; error bars, SEM.

Criterion 5 concerns the existence of a repair mechanism such as a conformist bias (an exaggerated tendency to copy the majority) (5, 14, 27, 28). To test this, we used a new device we called “the hexagon” (fig. S1B). By introducing already-copulating pairs along with a

Fig. 5. Criterion 5 of conformist mate-copying.

The nine demonstration treatments with various proportions of demonstrator females copulating with the pink males (x axis). Level of majority, proportion of the most commonly chosen male color during demonstrations; error bars, SEM; P values above or below bars, binomial tests of departure from random. The four treatments with a majority of pink (P) demonstrations differed from controls ($n = 348$; $P < 0.0004$). So did the four treatments with a majority of green (G) demonstrations ($n = 333$; $P = 0.042$), and these two blocks differed from each other ($n = 513$; $P < 0.0001$).

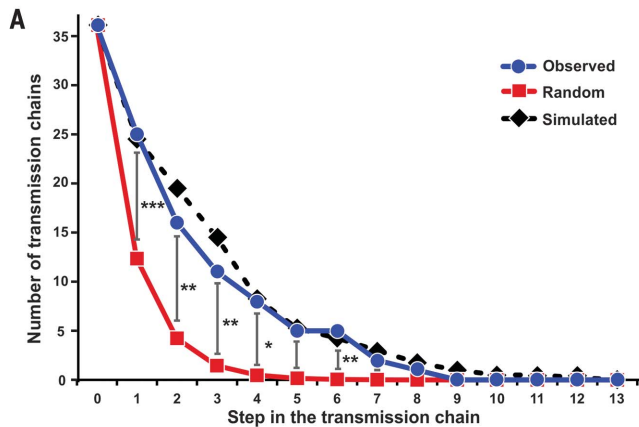
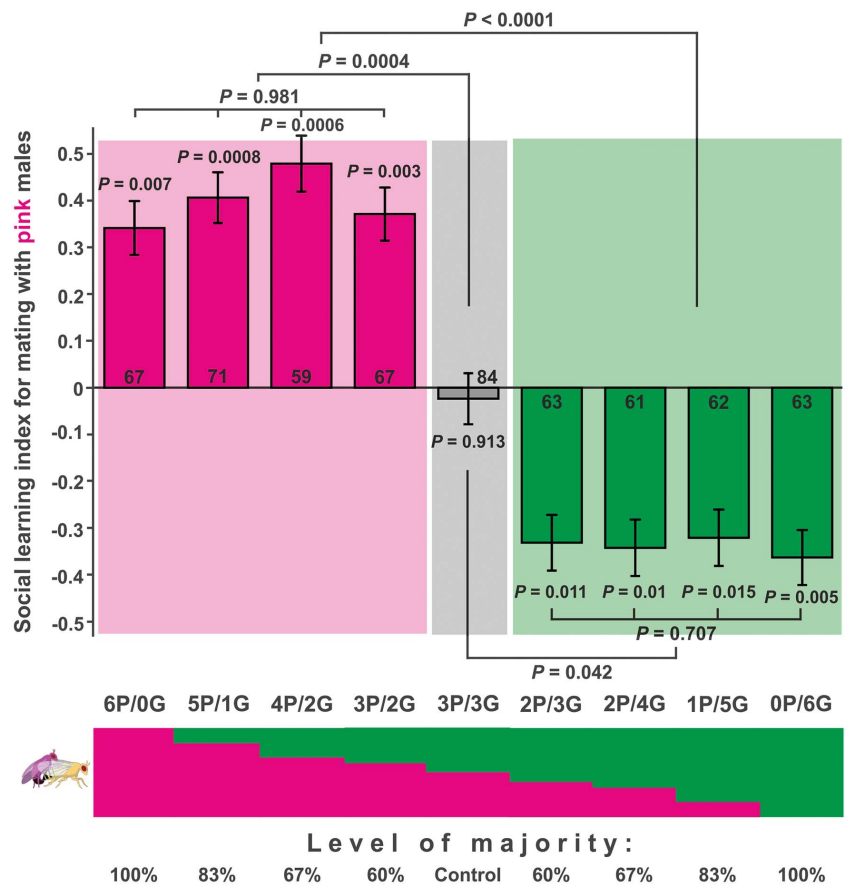
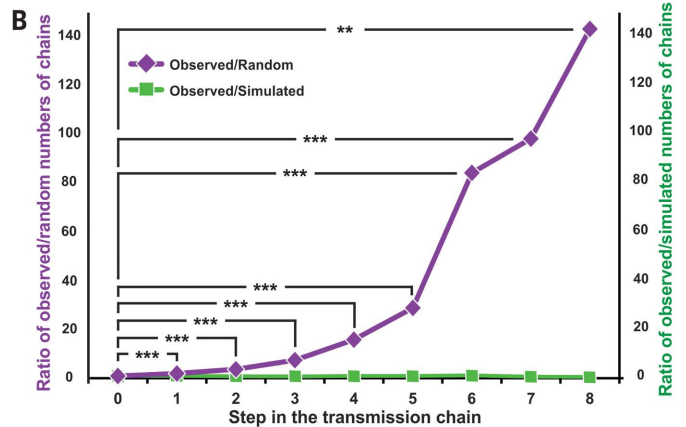


Fig. 6. Transmission chain in which observer females of one step became demonstrators for the next step.

(A) Number of the 36 chains that kept the initial preference for the indicated number of steps. Both experimental and simulation data involved only six observer females, which explains the relatively short persistence of the population preference (arrow in Fig. 7B). For each step, asterisks indicate the significance of the pairwise binomial test between the observed number of chains reaching that step (blue) and the number expected under random choice (red). Simulated data (black) were obtained under conditions mimicking experimental chains (see S1.5 and S1.6). Asterisks indicate the significance of the binomial test between



the observed and expected numbers of chains reaching the step in view of the number that reached the previous step. (B) Ratio of the observed number of chains reaching the indicated step to either the number predicted under random choice (purple) or the number produced by simulations (green). Asterisks indicate the significance of the binomial test between the observed number of chains reaching that step and the number predicted by chance from the initial number of 36 chains under the null hypothesis that females choose randomly (i.e., binomial test against a probability of 0.3438^x , where x is the step number) (see S1.5 and table S2). * $P < 0.05$; ** P value < 0.01 ; *** $P < 0.001$. More information is provided in S1.5 and table S2.

Fig. 7. A model of local tradition emergence in *D. melanogaster*.

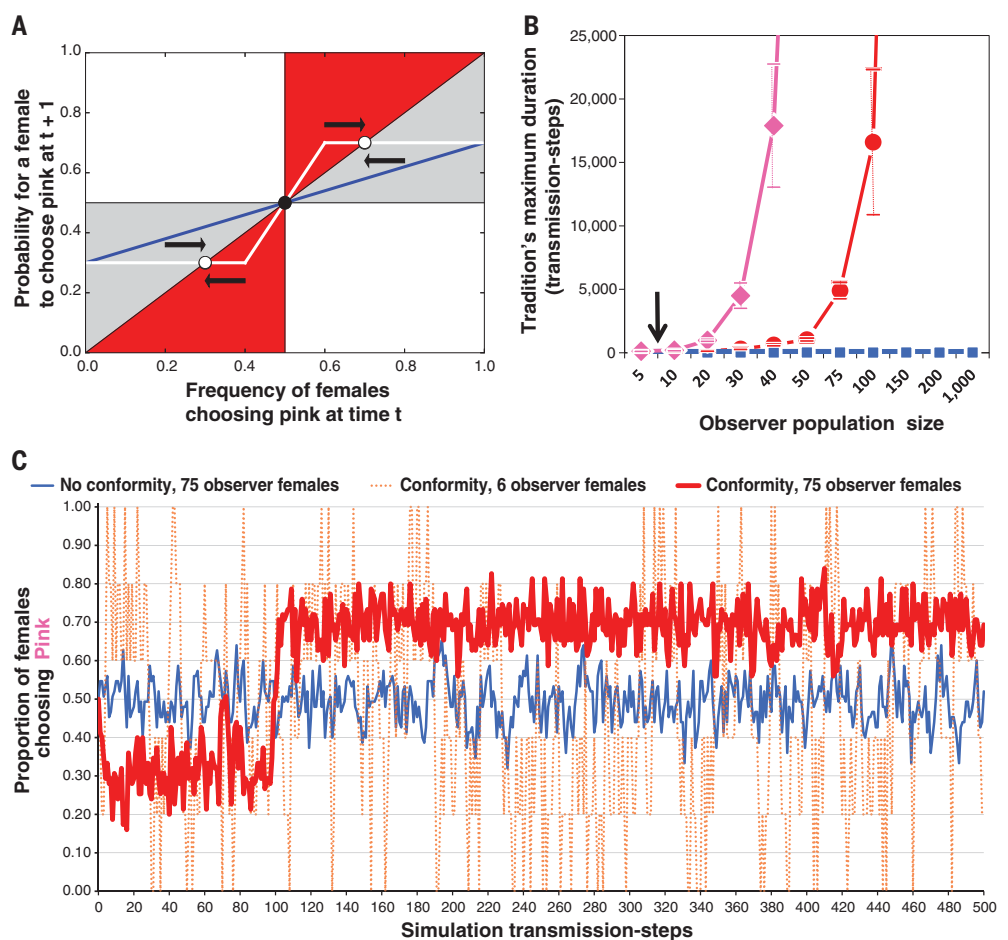
(A) Areas of the set of possible population mating preference response functions to demonstrations. Red areas, areas where observer females copy at a higher rate than the majority (i.e., exaggerate the choice of the majority), driving the population toward a preference for one color (white dots); gray areas, areas where observer females copy at a lower rate than the majority, driving the population toward the stable equilibrium of no preference (black dot); white areas, zones of anticonformity (a bias for males of the most commonly nonpreferred phenotype); blue line, without conformity; white line, the conformity function documented in Fig. 5.

(B) Effect of observer female number and mate-copying index on mean maximum population preference durations during five simulations of 100,000 transmission steps. Blue, simulations without conformity, as in the blue line of (A); red, simulations with conformity, as in the white line of (A), and with the mate-copying index set at 0.68 (i.e., the average in all experiments but long-term memory); pink, same simulations but with a mate-copying index of 0.78, as observed in long-term memory; vertical bars, SDs (most are too small to be visible); arrow, situation of the transmission chain performed in this study (Fig. 6). With transmission steps occurring every 24 hours (Fig. 3), the maximum tradition durations reported with conformity would correspond to thousands of *Drosophila* generations.

(C) Simulated dynamics over 500 transmission steps. Blue, dynamics without conformity [as in the blue line of (A)] with 75 observer females; red, dynamics with conformity with 75 observer females; orange, simulations with conformity and only six observer females, leading to frequent population preference shifts (this mimics the parameter of the transmission chain of Fig. 6). More results are shown in S1.6 and figs. S4 to S6.

male of the other color in each peripheral compartment of the hexagon, we manipulated the proportion of demonstrator females copulating with green or pink males (x axis of Fig. 5). We set up four situations with a majority of females copulating with pink males and four with a majority copulating with green males (100, 83, 67, and 60%), as well as one control in which three females copulated with green males and three with pink males.

As expected, control observer females did not build any mating preference (gray in Fig. 5), and replicates in which all six demonstrator females copulated with the same male color revealed strong mate-copying as in the above-described experiments. More surprisingly, as long as one male phenotype was chosen more often than the other (range, 100 to 60%), observer females learned to prefer males of the most commonly chosen phenotype (every color bar in Fig. 5 significantly differed from zero). We found no significant difference among the four treatments with a majority for one color [for the proportion of females copulating with pink as a class factor



or a continuous effect, $n = 264$ and $P = 0.981$ or 0.813 , respectively (Fig. 5, pink block); for green, $n = 249$ and $P = 0.707$ or 0.920 , respectively], indicating that social learning did not decline as the proportion of the most commonly chosen male decreased down to only 60%. Thus, mate-copying followed a step function, with females learning equally well to prefer the most commonly chosen male color whatever the level of majority (Fig. 5), revealing strong conformity in mate-copying and fulfilling criterion 5.

Fisher (29) speculated that by mating with their preferred males, females produce offspring that may inherit both the male trait and the mating preference in association, triggering the Fisher runaway process (29). In a theoretical population with A and B male phenotypes and in which more females mate with A males, females choosing B males will have sons of the non-preferred phenotype and daughters that will learn to prefer A males (as we show here). This will strongly diminish the fitness of nonconformist females (here choosing B males), thus favoring conformist females (here choosing A males). Con-

sequently, as soon as even the slightest detectable mating preference emerges within a population, conformist females are favored, as they transmit the most attractive trait to their male descendants while potentially culturally transmitting the preference for that same male trait to their daughters and/or to younger females.

Animal culture is classically studied through the existence of local traditions (1–4, 10). To study the capacity of the observed mate-copying in the fruitfly to generate persistent population preferences (i.e., traditions), we performed 36 transmission chains in hexagons in which the six observer females of one step were used as the six freely choosing demonstrators of the following step. A chain started with a demonstration where all six females chose the same male color and ended when the preference for the initially induced population preference became $\leq 50\%$. In this experiment, because the population had only six observer females, the frequency of shifts from a majority of females (four or more) choosing one color at one step to a majority of females choosing the other was high (0.2936) (S1.5 and

table S2). Nonetheless, experimental chains lasted much longer than predicted by chance, as revealed by Fig. 6A, in which the blue curve (representing observed behavior) is significantly higher than the red curve (representing behavior predicted by chance alone). These significant differences at each step accumulated so that the observed number of chains that reached the eighth step was 142 times as high as the number predicted by chance (Fig. 6B; more details are in S1.5). Thus, because of the effect of mate-copying, transmission chains lasted far longer than expected on the basis of chance alone.

The transmission chain experiment indicates that the social learning capacities in *Drosophila melanogaster* have the potential of stabilizing a preference for an arbitrary male phenotype at the scale of a population. However, for practical reasons, we cannot perform experiments under different conditions—for instance, under such conditions as large populations. Thus, to explore theoretically the effects of key parameters documented in testing criteria 1 to 5, we built a dynamical model of culture recapitulating our results. This model simulated a sequence of transmission steps in which observer females of one step became the demonstrators of the following step, as in our transmission chain experiment.

In infinitely large populations, the model is deterministic. A graphical analysis shows that nonconformist observer females (gray areas in Fig. 7A) always adopt an attenuated preference at each transmission step, leading initial preference for one male phenotype to fade away toward the black dot of Fig. 7A and generating dynamics as in the blue curve of Fig. 7C. Contrastingly, conformist learning [usually modeled with response functions entirely within the red areas of Fig. 7A, e.g., as in (27)] reinforces any initial preference, making population preference persistent. In *Drosophila*, however, parts of the response function (white line of Fig. 7A) are outside of this red area, making it difficult to extrapolate results from previous models.

In finite populations, the model is stochastic and cultural drift occurs, much as genetic drift occurs in finite populations. In small populations, odds that 50% or more of the flies make a copying “error” just by chance can be high, each time leading to a cultural shift in the population mating preference (Fig. 7C and figs. S4 to S6) and thus forbidding the establishment of a local tradition. For instance, with a mate-copying index of 0.68 (our observed average) (see S1.6) and six observer females, the probability that at each step at least half of the females choose the incorrect color by chance is 0.2936 (calculation in S1.5). This probability drops rapidly with increasing population size down to <0.001 and <0.0001 with 80 and 114 observer females, respectively (see S1.5). With a mate-copying index of 0.78 (as observed in long-term memory), odds that 50% or more observer flies make a copying error by chance are 0.139 for six flies and drop below 0.001 and 0.0001 with only 32 and 48 observer females, respec-

tively. Thus, the bigger the population and the higher the mate-copying index, the less frequently cultural shifts will occur and the longer the local population preference will persist, making it a cultural tradition.

To study this phenomenon, we built an individual-based model using the fruitfly response function (as in the white line of Fig. 7A). Simulations under the conditions of our transmission chain experiment (six observer flies, the initial preference at 100%, and ending when the initial preference drops to 50% or below) provided distributions of chain durations that closely matched the observed ones (black curve of Fig. 6A), which validates our model. In view of this validation, we then used this model to explore the effect of sets of parameters that would make transmission chain experiments infeasible for the capacity of the documented social learning function to produce persistent population preferences and thus cultural traditions. The form of conformity observed in *Drosophila* elicited long-lasting local preference (red line, Fig. 7C) corresponding to the stable equilibria of the infinite population model, with tradition stability strongly depending on both the population size and the mate-copying index [Fig. 7B and figs. S4 to S6; see also (30)]. For instance, these traditions potentially lasted for more than 100,000 transmission steps with 150 observer flies and a mate-copying index of 0.68 (red curve in Fig. 7B). The same result was obtained with only 50 observer females with a mate-copying index of 0.78 (the value observed with long-term memory) (pink curve in Fig. 7B). These population sizes are well below those observed in nature (S1.6). With one step representing 1 day (as suggested in Fig. 3), this would mean that traditions would theoretically last for thousands of fruitfly generations (see S1.5).

Culture used to be considered to be limited to humans. However, the range of species showing patterns of local variation in behavior akin to traditions now includes several mammals and birds (1–4). In this study, we found that fruitfly females express strong social learning (criterion 1) across age classes (criterion 2) that is memorized for sufficient time to be copied (criterion 3) and is trait-based (criterion 4) and conformist (criterion 5). With a model parameterized with the properties documented in our experiments, we found that these social learning properties can foster persistent local traditions in mating preference in populations of sizes common in nature. We have shown that population mate preference is maintained in transmission chains for longer than expected on the basis of chance in a way that closely matches our model predictions. Our lab experiments thus can be seen as a proof of concept in the lab that *D. melanogaster* has all the cognitive capacities and dispositions to transmit female mating preferences culturally across generations in ways that can elicit potentially long-lasting traditions of preferring an arbitrary male phenotype. This suggests that the taxo-

nomical range of culture may be much broader than ever before envisioned.

Our simulations also show that as predicted by theoretical consideration (15, 27, 31), a major characteristic for tradition emergence and maintenance is the existence of a correcting, or repair, mechanism such as trait-based conformity (5, 14, 27, 28, 32), as we empirically and theoretically document here. Conformity alone, however, does not necessarily result in culture and cultural inheritance (28). The fulfillment of a battery of other criteria is also necessary to generate persistent population preferences, eventually leading to cultural traditions. Although we adopted a demanding definition of culture jointly addressing all criteria discussed in the literature, the first explicit test of all these conditions simultaneously involves a nonsocial insect species. Cultural inheritance may thus have been a substantial part of evolutionary processes for extended periods of time.

Our study trait, mate choice, has considerable evolutionary implications, as strong local traditions in mating preference can amplify local sexual selection while hampering gene flow among populations with different traditions, favoring premating reproductive isolation and potentially speciation (33). In this mate-choice context, the Fisher runaway process can lead initially neutral male traits (such as those in our experiments) to quit neutrality as soon as chance generates some detectable statistical preference for one male phenotype. This starts a snowball effect favoring conformist females, a situation that was modeled decades ago (29, 33–36) but that still had little empirical evidence. The tradition then becomes part of the niche to which newcomers have to adapt by copying it (in German, *Gruppenzwang*, or “peer pressure”). Such strong selection for conformity in effect provides a general evolutionary explanation for mate-copying (18, 37) and speed learning (20) because it is essential for females to quickly grasp the local tradition before mating. More generally, our study shows one major way by which culture can affect evolution as it changes the selective social context of every individual.

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Competing interests: The authors declare no competing interests. **Data and materials availability:** Data, materials, associated protocols, and technical details, as well as the simulation code, are available to researchers desiring to replicate or expand studies of *Drosophila* mate-copying. Data and the R code for simulations can be downloaded at Dryad (38). The hexagon device can be purchased from Toulouse Tech Transfer and Paul Sabatier University.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/362/6418/1025/suppl/DC1
Materials and Methods
Figs. S1 to S11
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Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions

Etienne Danchin, Sabine Nöbel, Arnaud Pocheville, Anne-Cecile Dagaëff, Léa Demay, Mathilde Alphand, Sarah Ranty-Roby, Lara van Renssen, Magdalena Monier, Eva Gazagne, Mélanie Allain and Guillaume Isabel

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Trendsetting flies

Though once believed to be confined to humans, culture has now been demonstrated in many different animal species, from whales to parrots. Most such animals have high levels of cognition, but the basics of transmission and copying could easily occur in less cognitively advanced species. Danchin *et al.* show that mating culture can be passed on in *Drosophila* and model the process by which this occurs (see the Perspective by Whiten). Their results suggest that culture and copying may be much more widespread across the animal kingdom than previously believed.

Science, this issue p. 1025; see also p. 998

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