

Biased social transmission in *Drosophila* oviposition choice

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Abstract Within a group, animals adjust individual decisions to environmental conditions both through their own experience and by interacting with other animals. How individuals balance social vs. personal information may have a deep impact on their fitness, and this might be particularly relevant when individuals interact with conspecifics that carry different, or even conflicting, information. In animals, conformist strategy of social learning, defined by the tendency of individuals to disproportionately adopt the most commonly encountered social information, appears to be more widespread than previously thought. Here, we investigated whether females of the fruit fly, *Drosophila melanogaster*, conform their oviposition site choice to social cues coming from conspecifics. Groups of naïve “observer” flies were exposed to two oviposition media (banana or strawberry flavored) and to other “demonstrator” flies that were previously trained to prefer one of the two media. All flies were then tested for their oviposition preference. The preference of observer flies was highly sensitive to the social composition of the demonstrator group, and even the presence of a small proportion of individuals trained to oviposit on banana was enough to induce a biased preference for the banana medium. Our results suggest that *D. melanogaster* females combine their personal preference with social information to choose oviposition sites rather than showing social conformity.

Keywords *Drosophila* · Frequency-dependent bias · Oviposition

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Introduction

Egg-laying site selection is a central behavioral decision that strongly affects lifetime reproductive fitness. In *Drosophila* and other insects, this decision depends on a wide array of genetic and environmental factors (Fogleman 1979; Courtney and Chen 1988; van Delden and Kamping 1990; Possidente et al. 1999; Yang et al. 2008; Joseph et al. 2009) and can be modified by larval or adult experience (Jaenike 1982; Hoffmann 1985; Mery and Kawecki 2002; Sarin and Dukas 2009). In a recent study, Battesti et al. (Battesti et al. 2012) showed that *Drosophila* females may also use social information to select oviposition substrates and that these socially acquired preferences can be transmitted within groups. When naïve observer female flies interacted with a group of demonstrator flies that were all trained to prefer a specific flavor of oviposition medium, the naïve females showed an increased preference for the same flavor. However, in nature, animals can face varied and conflicting sources of information. A number of recent studies have used a range of biological model systems from fish to human and types of behavioral decisions to explore how animals integrate information from multiple demonstrators (Pike and Laland 2010; Haun et al. 2013; Stienessen and Parrish 2013; van de Waal et al. 2013). Previous studies have shown that animals do not use social learning indiscriminately but rather show selective rules depending on the environment and social context (Laland 2004; Kendal et al. 2009; Rendell et al. 2010; Grüter et al. 2013). As a consequence, information should not spread randomly within a group but may depend on the way individuals use social information. Boyd and Richerson (Boyd and Richerson 1985) proposed three types of departure from simple linear transmission called transmission biases: indirect, direct, and frequency-dependent. Indirect bias occurs when individuals learn from demonstrators depending on their status as kin and familiarity affiliations, age, health, or dominance. Direct

bias defines individuals' facilitation to learn a stimulus inherently attractive, i.e. any slight occurrence of this stimulus within the social environment will disproportionately affect individual behavior. This was found, for example, in rats for transmission of food preference (Chou and Richerson 1992). A single demonstrator signaling the use of a given preferred diet in a large set of demonstrators resulted in a disproportionate food preference response by naïve observer rats. Finally, frequency-dependent bias reflects an observer tendency to adopt the behavior of the majority within a group (positive frequency dependence) or of the minority (negative frequency dependence). Conformity has been observed in several studies (Kendal 2004; Pike and Laland 2010; van de Waal et al. 2013). It is a form of positive frequency-dependent bias—defined as the tendency to disproportionately adopt the most commonly encountered social information. Imitating the majority can be an adaptive strategy, in particular, if the success of cultural traits strongly depends on the local circumstances. The potential impact of conformism on behavioral evolution and group dynamic has recently received considerable attention (Henrich and Boyd 1998; Peña et al. 2009; Molleman et al. 2013). However, most studies have mainly focused on some group-living species in which the fitness of individuals is strongly dependent on group cohesion. Despite the potential impact of these different biases on the dynamic of social information transmission within groups, we still know very little about how widespread each occurs and how animals weigh personal and social information (Kendal 2004; Grüter et al. 2013; Leadbeater and Florent 2014). Using *Drosophila* as a model system, Battesti et al. (2012) found that oviposition site choice could be transmitted from a majority of demonstrators to a minority of naïve observers, suggesting the use of a frequency-dependent strategy of social learning. Based on a similar experimental design, we present an experiment investigating how *Drosophila* uses social learning to make oviposition site choice decisions when interacting with different sources of social information.

Materials and methods

Fly stocks

All flies used were from a *D. melanogaster* strain collected in Chavroches (France) in 2009. Flies were raised in the lab under high population size in vials (around 100 flies per vial) containing standard axenic medium in a 12-h/12-h light/dark cycle at 21 °C. We used 5-day-old females that were separated from males 1 day before the experimental treatment. Females typically mate within 24–48 h postemergence, and thus at this stage, all females were fully matured and mated. To differentiate demonstrators and observers, we cut a piece of each observer fly's wings under ice anesthesia. A previous

experiment revealed no difference in learning performance between wing-cut and normal flies (Battesti et al. 2012).

Experimental procedure

The general experimental procedure followed the one described by Battesti et al. 2012 (Battesti et al. 2012). The protocol can be divided into three consecutive phases:

Training phase

We first trained, during 8 h, groups of “demonstrator” flies to preferentially lay eggs on one of two flavored oviposition media. Groups of eight flies were first introduced to a 120×50×90 mm plastic cage and then were given the choice between two oviposition substrates—a banana or strawberry medium—one of which was supplemented with 3 g/L of quinine, a bitter and aversive gustatory compound. These media were prepared from 20 g/L sucrose, 10 g/L agar, and 6 mL/L artificial banana or strawberry flavor (Gazignaire SA) and poured into a 35-mm Petri dish. Previous experiments show that, without any quinine and at this odor concentration, flies have a slight preference for the banana medium, with some day-to-day variation (on average 57 % of the eggs are laid on banana ($N=40$) (Battesti et al. 2012)). In half of the replicates, quinine was added into the banana-flavored medium (flies were trained to lay eggs on strawberry), and in the other half it was added to the strawberry-flavored medium (flies were trained to lay eggs on banana). In a control treatment, “demonstrator” flies were not trained but just placed with the two flavored media free of quinine during the training phase.

Transmission phase

We then initiated a “transmission phase” during which naïve observer flies were given the choice of the two types of oviposition media and allowed to interact with different ratios of demonstrators previously trained to lay eggs on banana vs. strawberry or just familiarized with them.

The transmission phase began after a 12-h training phase. The demonstrator flies were moved into a new cage containing four naïve observer flies and then given the two flavored oviposition media (neither contained quinine). The observer and demonstrator flies were left to interact and lay eggs for 4 h.

During this transmission phase, we manipulated conflicting social information by varying the ratio of demonstrators trained to lay eggs on each medium. We established the following seven ratios (B = trained to lay eggs on banana, S = trained to lay eggs on strawberry): 8B ($N=48$), 6B:2S ($N=44$), 5B:3S ($N=42$), 4B:4S ($N=41$), 3B:5S ($N=44$), 2B:6S ($N=44$), and 8S ($N=41$) plus the control treatment: 8C ($N=61$).

Test phase

The “test” phase involved testing the oviposition preference of groups of demonstrators and observers separately over 4 h. After the transmission phase, flies were moved to new cages that contained both flavored media (again without quinine). We measured oviposition preference as the proportion of eggs laid on banana. We previously found no oviposition site preference differences whether flies were tested in groups of 8 or 4 females (Battesti et al. 2012) suggesting, under these circumstances, no effect of flies density on oviposition choice. In order to understand how social transmission is affected by group composition, following Chou and Richerson (Chou and Richerson 1992), we tested whether the best fit to the relationship between the proportion of eggs that groups of flies laid on banana (PB) and the demonstrator ratio (DR) was linear, quadratic, or cubic. These three types of models correspond to:

- Linear: for observers, a linear relationship would suggest no bias in social transmission. For demonstrators groups, it would suggest that each individual chose egg-laying medium accordingly to its own individual experience during the training phase.
- Quadratic: for observers, it would suggest that a direct bias is involved in social transmission. Any small change in the social composition of the demonstrator group would induce a strong modification of oviposition preference toward a specific oviposition media. For demonstrators, it would also suggest a direct bias either during the training phase through individual learning or during the transmission phase through social interactions.
- Cubic: for observers, it would suggest that a frequency-dependent bias occurred during the transmission phase (including conformity bias). Preference for one or the other media would depend on the majority of demonstrators conditioned to prefer this medium. Similarly, for demonstrators, it would suggest the occurrence of a frequency-dependent bias either during the training phase or during the transmission phase.

We applied a generalized linear model assuming a binomial error structure to analyze the effect of demonstrator group composition on oviposition choice during the test phase (Crawley 2007). Statistical calculations for the generalized linear model were performed by using IBM SPSS statistics V20. The best fit model was determined by the Akaike information criterion (AIC) choosing the AIC with the least score as the best fit.

Comparison of the proportions of eggs laid on banana among the demonstrators’ ratio treatments was performed using planned contrasts and sequential Bonferroni correction.

In a subset of random replicates (50 %) from the 8B, 6B:3S, 2B:6S, 8S, and 8C treatments, we counted the number

of eggs laid by demonstrators and observers on each oviposition medium during the transmission phase. We introduced a random subset factor in a linear model to check whether flies of these replicates behaved differently from flies of the other replicates during the test phase. The random subset factor was not significant ($F_{1,606}=0.004$; $P=0.95$).

Results

During the test phase, the preference to lay eggs on the banana medium depended on the demonstrator ratio. For demonstrators, as expected, the proportion of eggs laid on banana at the group level followed a positive linear relationship with the number of demonstrators trained to lay eggs on banana ($X^2=14.1$, $P<10^{-3}$; Fig. 1). Quadratic model regression did not provide a better fit ($AIC_{\text{quadratic}}-AIC_{\text{linear}}=342$). For observers, the proportion of eggs laid on banana during the test phase also followed a significant linear relationship with the demonstrator ratio, but a quadratic polynomial regression provided a better fit (linear regression: $X^2=14.9$, $P<10^{-3}$; quadratic regression: $X^2=10.9$, $P<10^{-3}$; $AIC_{\text{quadratic}}-AIC_{\text{linear}}=-286$). Cubic model regression did not provide a better fit ($AIC_{\text{cubic}}-AIC_{\text{quadratic}}=429$).

Post hoc procedure applied on observer flies preference during the test phase showed that flies had the same strong preference for the banana-flavored medium independently of the demonstrator ratio except when all demonstrators were

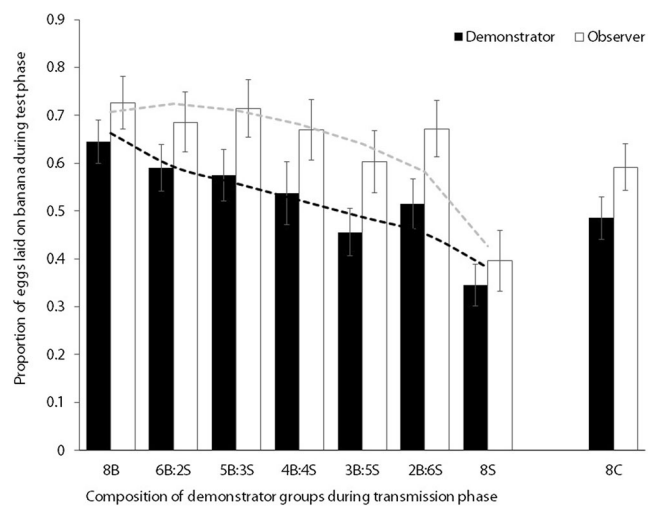


Fig. 1 Proportion of eggs laid on the banana-flavored medium during the test phase as a function of the social composition of the demonstrators group during the transmission phase. Dotted lines represent the predicted values of the linear relationship (black dots, demonstrators) or of the quadratic relationship (gray dots, observers). Demonstrators’ group compositions: B: demonstrators trained to lay eggs on banana media, S: demonstrators trained to lay eggs on strawberry media, C: control treatment ($N_{8B}=48$, $N_{6B:2S}=44$, $N_{5B:3S}=42$, $N_{4B:4S}=41$, $N_{3B:5S}=44$, $N_{2B:6S}=44$, $N_{8S}=41$, and $N_{8C}=61$). Error bars are standard errors of the mean

trained to lay eggs on strawberry (Fig. 1). In this case, observer flies showed significant preference for strawberry. The proportion of eggs laid by trained demonstrators in 8B and 8S treatment were significantly different from the control group, as well as their observers with a tendency between 8B and 8C suggesting modification of oviposition preference in both direction (Planned comparison with sequential Bonferroni correction between demonstrators 8B and 8C: 0.16 ± 0.066 , $P=0.04$; demonstrators 8S and 8C: -0.14 ± 0.066 , $P=0.04$; observers 8B and 8C: 0.135 ± 0.070 , $P=0.067$; observers 8S and 8C: -0.195 ± 0.079 , $P=0.013$, Fig. 1).

The subset of replicates for which eggs were counted during the transmission phase showed that flies mainly laid eggs on strawberry in the 2B:6S and 8S treatments (comparison with control 8C: *t* test, 2B:6S: $t=-2.37$, $P<10^{-3}$; 8S: $t=3.09$, $P=0.007$, Fig. 2) and flies mainly laid eggs on banana in the 8B and 6B:2S treatment (*t* test, 2S:6B: $t=10.16$, $P<10^{-3}$; 8B: $t=21.7$, $P<10^{-3}$, Fig. 2).

Discussion

In this study, we investigated how *Drosophila* responds to conflicting social information in an oviposition site choice task. We exposed naïve observer flies to different ratios of demonstrator flies trained to lay eggs on either a banana- or a strawberry-flavored medium. During the transmission phase, observer flies were able to interact with the different demonstrators and experience conflicting social information but were also able to individually directly experience the two flavored media. During the test phase, oviposition preference of

demonstrator and observer flies was tested separately. In the demonstrator groups, there was a linear relationship between the proportion of eggs laid on banana and the proportion of flies previously trained to lay eggs on banana. Interestingly, observer flies did not behave the same way. The preference for banana was low when observer flies had previously interacted with demonstrators that were all trained to lay eggs on strawberry but showed a disproportionately stronger preference when observers had previously interacted with a demonstrator group in which even just two out of eight flies had been trained to lay eggs on banana. This strong bias toward banana in observers' response seems to depend directly on group composition. Social transmission from demonstrators to observers varied nonlinearly with the demonstrators ratio: observers acquired a preference for banana when at least 25 % of the demonstrators were trained on banana, while they acquired a preference for strawberry when at least 75 % of the demonstrators were trained on strawberry. Moreover, during social transmission phase, flies in the 2B:6S treatment primarily laid much more eggs on strawberry than the control treatment which suggests that the behavioral response observed during the test phase may not reflect a simple aggregation phenomenon on banana during the transmission phase.

Observers were strongly influenced by the social environment, and their shift to a preference for banana makes their response to demonstrators' ratio close to a quadratic curve as predicted by Chou and Richerson (Chou and Richerson 1992). Interestingly, demonstrators did not show the same response. The linear trend observed in demonstrators would suggest that, unlike observers, each individual behaved according to its personal information and ignored the social environment even when the average demonstrators' preference was strongly biased toward one of the odorants. As initially proposed by Boyd and Richerson (Boyd and Richerson 1988), individuals should rely on social information when they lack personal information on the outcome of their behavioral decision. However, prior personal information should prevent an individual to modify its behavior by copying the choice of others when the success of such choice is uncertain. We observed a disproportionate shift in preference for a specific flavor in response to demonstrator preference for that flavor. In this apparatus, observers could acquire social information using demonstrators' oviposition choice behavior or by direct interaction. Interestingly, behavioral differences in oviposition choice between the transmission phase and the observers' test phase would support the second option. In the 2B:6S treatment, flies (groups composed of demonstrators and observers) mainly laid eggs on the strawberry medium during the transmission phase, but during the test phase, observers alone laid mainly eggs on banana and thus did not copy the behavior observed during the previous phase. In a previous study (Battesti et al. 2012), we also showed that eggs laid on a medium were not used as social cue by observers. Further

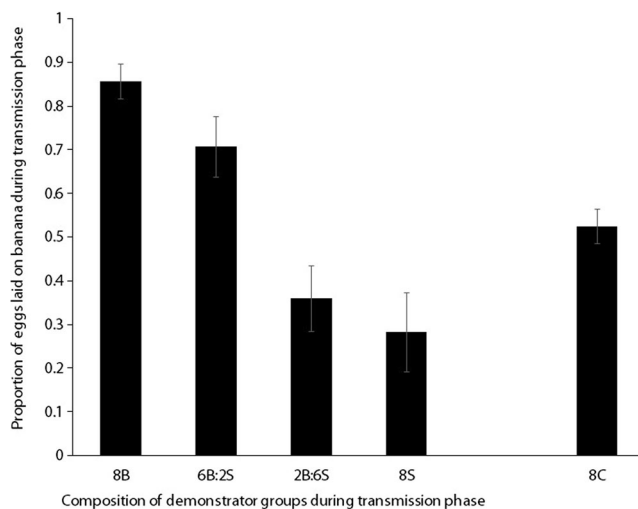


Fig. 2 Proportion of eggs laid on the banana-flavored medium during the transmission phase as a function of the social composition of the demonstrators group during this same phase. Demonstrators' group compositions: B: demonstrators trained to lay eggs on banana media, S: demonstrators trained to lay eggs on strawberry media, C: control treatment. $N_{8B}=20$, $N_{6B:2S}=18$, $N_{2B:6S}=17$, $N_{8S}=17$, and $N_{8C}=61$. Error bars are standard errors of the mean

investigation needs to be done to better understand this phenomenon.

Social modification of preference was strongly skewed by the presence of even a few banana-trained demonstrators. Strawberry was only preferred when all demonstrators were trained to prefer this flavor. Following Boyd and Richerson (Boyd and Richerson 1985) definition, female flies showed a direct bias social learning for their oviposition site choice. This raises questions about the conditions under which social information can spread within groups and how innate preference for a flavor may affect social transmission bias. One potential explanation is that due to the differential caloric value of natural banana and strawberry for larval development, strawberry may only be considered a suitable oviposition medium when all demonstrators avoid banana, which may be a reliable sign of toxicity.

Individual decision making is the result of complex interactions between different social and personal information sources in response to environment variation. Experiments such as ours presented here show that social information may trigger rapid, and biased, changes in resource preference. Accounting for social interactions within populations will enhance our understanding of variation within a species' ecological niche.

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