

Learning magnifies individual variation in heterospecific mating propensity

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ARTICLE INFO

Article history:

Received 7 March 2009
 Initial acceptance 9 April 2009
 Final acceptance 18 May 2009
 Published online 16 July 2009
 MS. number: A09-00143R

Keywords:

assortative mating
Drosophila persimilis
Drosophila pseudoobscura
 fruit fly
 learning

Recent research indicating learning in the context of sexual behaviour in fruit flies suggests that learning could increase levels of assortative mating between partially diverged populations. We present a graphic model examining the role of learning and a series of experiments evaluating assumptions and predictions of the model. We found that male *Drosophila persimilis* that previously succeeded in mating with females of the sibling species, *D. pseudoobscura*, did not have a higher heterospecific mating success than males that were either virgin or previously mated with conspecific females. On the other hand, female *D. pseudoobscura* with apparently strict mating criteria, which rejected heterospecific males, were also more likely to reject conspecific males than were females inexperienced with males. Finally, *D. persimilis* males previously rejected by heterospecific females courted significantly less and had half as much heterospecific mating success as males previously accepted by heterospecific females. These results, combined with previous evidence demonstrating that males rejected by heterospecific females learn to avoid courting such females, indicate that learning can increase phenotypic divergence between populations with partial pre-mating isolation.

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The recent surge in research on mechanisms leading to speciation (Coyne & Orr 2004; Grant & Grant 2008; Price 2008) has been accompanied by renewed interest in the role of learning in population divergence (e.g. Lachlan & Servedio 2004; Magurran & Ramnarine 2004; Beltman & Metz 2005; Verzijden & ten Cate 2007; Servedio et al. 2009). New information regarding learning in the context of courtship and mate choice in fruit flies (*Drosophila* spp.) has provided exciting fresh opportunities for examining effects of learning on processes leading to population divergence in one of the key model organisms used in research on speciation (e.g. Coyne & Orr 1989; Noor & Feder 2006). Specifically, work with two pairs of sibling species, *D. melanogaster*–*D. simulans* and *D. persimilis*–*D. pseudoobscura* has indicated that males that experience rejection by heterospecific females rapidly learn to reduce courtship of such females (Dukas 2004b, 2008, 2009).

Whereas the studies indicating learning in the context of sexual behaviour in fruit flies suggested that learning can increase assortative mating, the experimental protocols used actually simulated interactions between two species that are already fully reproductively isolated because the experience phases always included heterospecific rejection. To understand the role of learning in the divergence of populations that are only partially isolated, however,

we have to simulate the realistic scenario in which some proportion of the males succeed in acquiring heterospecific mates while the majority fail. Learning could contribute to population divergence even under such realistic settings, and here we examine this possibility using a graphical model and empirical tests.

Suppose that two populations that are partially reproductively isolated come into contact in sympatry and that males of population A encountering females of population B court them as much as they court females of population A. Furthermore, suppose that heritable variation in attractiveness among the males and in permissiveness among the females determine the small fraction of individuals that accomplish interpopulation matings. Figure 1 presents a graphical representation of this scenario following standard signal detection theory (Green 1966; Wiley 1994) as applied explicitly to fruit fly courtship (Dukas et al. 2006). Heritable individual variation in attractiveness and permissiveness is well known in a variety of species including fruit flies (Manning 1967; Carracedo & Casares 1985; Jamart et al. 1993; Andersson 1994; Jennions & Petrie 1997). Such interpopulation interactions would result in a minority of males and females producing hybrids with presumably lower fitness and most males being rejected by females of the other population. These rejected males would learn to avoid females of population B and hence reduce their future probability of heterospecific mating (Fig. 2). That is, learning could magnify the effects of heritable variation and this could facilitate population divergence over time.

To evaluate the above model, we conducted a series of experiments with the sibling species *D. persimilis* and *D. pseudoobscura*.

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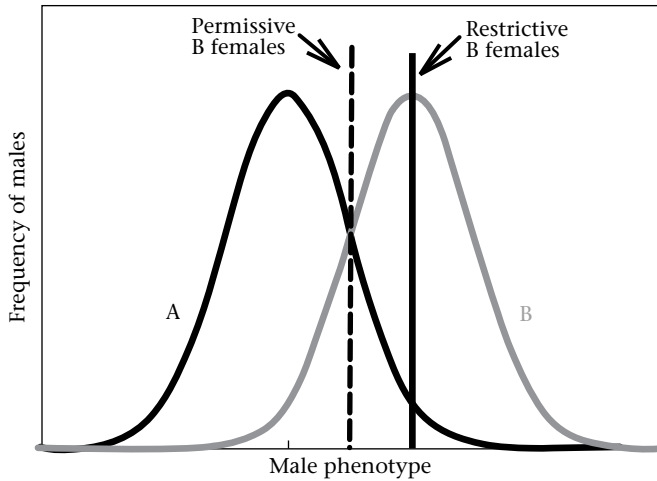


Figure 1. Hypothetical frequency distributions of male phenotypes in two diverging populations, A and B, and two hypothetical mating criteria of females in population B. The X axis represents the set of traits determining the perceived phenotype of males by females of population B. The restrictive females are more likely to reject both heterospecific and conspecific males than are the permissive females.

Flies of these recently diverged species look alike and are similar in size, but the males differ slightly in their cuticular hydrocarbons and courtship songs. Heterospecific matings are frequent in the laboratory, especially between naïve pairs of allopatric female *D. pseudoobscura* and male *D. persimilis* (e.g. Mayr 1946; Noor 1995; Dukas 2008). We tested three predictions addressing, respectively, individual variation in male attractiveness to heterospecific females, individual variation in female permissiveness, and whether learning can magnify individual variation in mating success. Specifically, we predicted that, first, males that had previously succeeded in mating with heterospecific females would have a higher heterospecific mating success than either virgin males or males that had previously mated with conspecific females. Second, females that had rejected heterospecific males, which presumably possess a more restrictive mating criterion (Fig. 1), would be more likely to reject conspecific males than randomly chosen virgin females. Finally, males that had been rejected by heterospecific females would show less courtship towards and

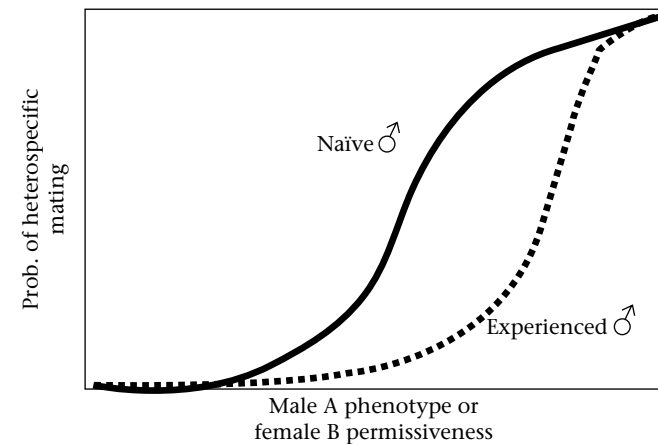


Figure 2. Probability of heterospecific mating success by population A males as a function of either their own phenotype or the permissiveness of population B females. Rejection experience changes the phenotype of population A males, which reduces their subsequent probability of heterospecific mating.

obtain fewer matings with such females compared to males that had previously been accepted by heterospecific females.

GENERAL METHODS

We used stocks of *D. persimilis* and *D. pseudoobscura* provided by the *Drosophila* Tucson Stock Center, Tucson, Arizona, U.S.A. *Drosophila pseudoobscura* were initially collected in Tucson, Arizona in 2004, and *D. persimilis* were initially collected on Santa Cruz Island, California, U.S.A. in 2004. Arizona is outside the range of *D. persimilis*, which only occurs along the Pacific Coast of North America, where the two species coexist in sympatry (Dobzhansky & Powell 1975; Markow & O'Grady 2005). The flies were maintained in large population cages housed in distinct environmental chambers and fed standard fly medium.

We collected virgin flies within 8 h of eclosion. The flies were anaesthetized with CO₂, separated by sex, placed in groups of 20 in 40 cm³ vials, each containing 5 cm³ of standard fly medium, and kept in the environmental chambers. One day before the start of an experiment, we moved males into individual vials containing standard food medium because such isolation increases male courtship and mating success (Noor 1997).

In all the experiments, the heterospecific pairings involved male *D. persimilis* and female *D. pseudoobscura* because such pairings result in a higher frequency of heterospecific matings than the alternate pairings (Noor 1995). Each experiment consisted of two phases with the second phase being the test in which we monitored matings in all the vials and conducted continuous behavioural observations on a sample of the vials. All observations were conducted by observers blind to fly treatment. We used logistic regression to analyse the mating data and ANOVAs on arcsine square-root transformed courtship proportions. The transformed data met ANOVA assumptions. We attempted to maximize the sample sizes for each experiment but the number of trials varied among experiments owing to insufficient availability of flies and fewer than predicted heterospecific matings.

Experiment 1a: Males Mated with Heterospecific Females versus Virgin Males

Methods

Here we tested for repeatable variation in male heterospecific mating success (Fig. 1). We predicted that *D. persimilis* males that had previously mated with heterospecific females would have a higher heterospecific mating success than virgin *D. persimilis* males. We also predicted that the proportion of time spent courting by males in each of the treatments would be similar because both male treatments should perceive the females as highly desirable mates. Male *D. persimilis* can readily mate conspecifically at least twice within a few minutes (Dukas 2009, unpublished data). We used 6-day-old females and 4-day-old males and conducted 240 trials with 120 males per each of the two conditions. Each male was subjected to two phases detailed below.

Phase 1. Randomly selected males were placed one per vial either alone or with a heterospecific female. The virgin males and the males that completed heterospecific matings were used in phase 2.

Phase 2. At the end of each heterospecific mating, the mated male was placed in a fresh vial along with two virgin heterospecific females. Then a matched virgin male from phase 1 was also placed in a fresh vial along with two virgin heterospecific females. All vials were monitored for 30 min and mating was recorded using a custom-designed computer program.

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