



Mate copying in *Drosophila melanogaster* males

Sabine Nöbel^{a,*}, Mélanie Allain^a, Guillaume Isabel^b, Etienne Danchin^a

^a CNRS, Université de Toulouse III Paul Sabatier, IRD, UMR 5174, EDB (Évolution & Diversité Biologique), Toulouse, France

^b CNRS, Université de Toulouse III Paul Sabatier, UMR 5169, CRCA (Centre des Recherches sur la Cognition Animale), Toulouse, France

ARTICLE INFO

Article history:

Received 20 October 2017

Initial acceptance 21 December 2017

Final acceptance 30 March 2018

MS. number: 17-00843R

Keywords:

fruit fly

male mate copying

public information

social learning

To assess potential mates' quality individuals can observe sexually interacting conspecifics. Such social information use is called mate copying and occurs when observer individuals witnessing sexual interactions of conspecifics later show a mating preference for mates that were seen mating. Most studies have focused on female mate copying, as females are usually the choosy sex. However, much less is known about the existence of male mate copying, probably because of the usual strong asymmetry in sex roles. Mate copying has been documented in female *Drosophila melanogaster*, and here we report on experimental evidence for mate copying in males of this species in which females can actively reject males and prevent copulation. As mate choice implies high costs for males we assumed that they perform mate copying as well. We created two artificial female phenotypes by randomly dusting females with green or pink powders, and virgin naïve observer males were given the opportunity to see a demonstrator male choosing between a pink and a green demonstrator female. Immediately afterwards, observer males were given the choice between two new females, one of each colour. To circumvent the difficulty of determining actual male mate preference, we used two complementary indices of male mate choice, both of which provided evidence for male mate copying. Informed observer males showed a bias towards females of the colour they saw being chosen during demonstrations, while uninformed males chose randomly between pink and green females. This suggests that male fruit flies can also perform mate copying. Although significant, our results in males were less clear-cut than in females in previous studies. However, like females, *D. melanogaster* males can mate copy based on a single observation. The importance and generality of such mate copying abilities in nature, and their potential impact on the evolution of *Drosophila* and probably other invertebrates, need further exploration.

© 2018 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

To evaluate potential mates, animals of a wide range of taxa have been shown to use public information (i.e. information that is accessible to all individuals; Wagner & Danchin, 2010). In particular, individuals can assess the quality of potential mates from their mating performance. One form of such social learning is mate copying (Danchin, Giraldeau, Valone, & Wagner, 2004; Gibson & Höglund, 1992; Wade & Pruett-Jones, 1990) which occurs when an observer uses the mating performance of potential mates to develop a sexual preference. Typically, in mate copying, an observer shows a mating preference for mates that it saw being preferred by conspecifics (Pruett-Jones, 1992; reviewed in; Vakirtzis, 2011). Mate copying can be either at the individual level (individual-based

copying, Bowers, Place, Todd, Penke, & Asendorpf, 2012) or at the phenotypic level (trait-based copying, Bowers et al., 2012). In the former case, the preference is only for the specific individual that was seen successfully attracting a partner, while in the latter case the preference is for any potential mate of the same phenotype.

Mate copying can be a fast and safe strategy to gather integrative information about the quality of potential mates (Westneat, Walters, McCarthy, Hatch, & Hein, 2000; reviewed in; Witte & Nöbel, 2011). It has been experimentally demonstrated in several species of birds (Galef & White, 1998; Gibson, Bradbury, & Vehrencamp, 1991; Höglund, Alatalo, Gibson, & Lundberg, 1995; Knier et al., 2015), mammals (Bowers et al., 2012; Galef, Lim, & Gilbert, 2008; Waynforth, 2007), fish (reviews in Danchin et al., 2004; Witte, Knier, & Kureck, 2015) and one insect species (*Drosophila melanogaster*; Dagaëff et al., 2016; Mery et al., 2009; Monier, Nöbel, Isabel, & Danchin, 2018). Most published experiments tested the effect of positive social information (i.e. success in attracting mates), but it has also been shown that the negative

* Correspondence: S. Nöbel, CNRS, Université de Toulouse III Paul Sabatier, IRD, UMR 5174, EDB (Évolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse Cedex 9, France.

E-mail address: sabine.noebel@univ-tlse3.fr (S. Nöbel).

social information provided by the rejection of a potential mate can also elicit mate copying with observers tending to reject previously rejected individuals (Witte & Ueding, 2003).

Most studies have reported on female mate copying as females are usually considered the choosier sex (Trivers, 1972) because they usually invest more in the production of each descendant (Kokko & Johnstone, 2002). However, although males are expected to be less choosy than females, they may still benefit from distinguishing between receptive and nonreceptive females to avoid courting reluctant females or the costs of sperm production and/or parental care (reviews in Dewsbury, 1982; Kokko & Jennions, 2008; Nakatsuru & Kramer, 1982). Accordingly, evidence is accruing that males also can have mating preferences (reviewed in Verzijden et al., 2012). Nevertheless, studies of mate copying in males remain relatively rare and often concern species in which males invest significantly in reproduction. For instance, male mate copying has been shown in the deep-snouted pipefish, *Syngnathus typhle*, a sex role-reversed species, in which males but not females mate-copy (Widemo, 2006). Similarly, in the darter *Etheostoma flabellare*, a species in which males invest in reproduction by guarding the nest site and caring for developing eggs, males but not females show mate copying (Moran, von Ende, & King, 2013). However, male mate copying can also exist in species without parental care, and in which both males and females perform mate copying. This is the case in three fish species, the sailfin molly, *Poecilia latipinna* (Witte & Ryan, 2002), the Atlantic molly, *Poecilia mexicana* (Bierbach, Kronmarck, Hennige-Schulz, Stadler, & Plath, 2011; Heubel et al., 2008) and the darter *Etheostoma zonale* (Moran et al., 2013).

Mating and egg production are costly in *D. melanogaster* females (Chapman, Liddle, Kalb, Wolfner, & Partridge, 1995; Fowler & Partridge, 1989; Partridge, Green, & Fowler, 1987). In this species there is no documented parental care, but males are known to produce large and costly sperm cells (1.91 ± 0.001 mm) and have testes representing up to about 5% of their body mass (Pitnick, 1996); sperm depletion starts after a single copulation event (Demerec & Kaufman, 1941; Lefevre & Jonsson, 1962; Loyau, Blanchet, Van Laere, Clobert, & Danchin, 2012). Males also display elaborate and costly courtship (Spieth, 1974); this plus the transfer of about 4000 large and costly sperm cells (Gilbert, 1981) during the 20 min of a typical copulation (Pavkovic-Lucic, Lucic, Milicic, Tomic, & Savic, 2014) decrease the life span of sexually active males (Cordts & Partridge, 1996; Partridge & Farquhar, 1981). Thus, the asymmetry between male and female investment in each descendant appears much lower in *Drosophila*, and especially in *D. melanogaster*, than in other species. Furthermore, *D. melanogaster* males show adaptive mate choice and mate preference learning (Byrne & Rice, 2006; Dukas, 2004, 2009). For instance, males can distinguish mated from virgin females, direct their courtship more specifically to virgins and learn to associate the pheromone *cis*-vaccenyl acetate (cVA) with mated females (Ejima et al., 2007; Keleman, Vrontou, Krüttner, Yu, Kozaric-Kurtovic & Dickson, 2012). In *Drosophila*, males can also visually associate an arbitrary trait such as eye colour with female mating status (Verzijden, Abbott, von Philipsborn, & Loeschke, 2015).

All these biological characteristics led us to expect mate choice to be partly mutual in *D. melanogaster*. This situation would put males under constraints that are closer to those of females of species with stronger asymmetry in the investment in a single offspring. We could thus expect them to adopt female-like strategies, and we speculated that they may perform mate copying. The question of whether we could detect it, however, remained open because females of this species often actively reject courting males by kicking, wing fluttering, depression or elevation of the tip of the abdomen, ovipositor extrusion or decamping (Lasbleiz, Ferveur, &

Everaerts, 2006; Spieth, 1974), while the reverse is never observed. This suggested that it might be more difficult for males than females to copulate with their preferred partner, thus hampering our capacity to detect male mate preferences and, thus, male mate copying in this species.

In the current study, following the above considerations, we tested whether mate copying exists in *D. melanogaster* males. We assumed that copying would be trait based rather than individual based (Bowers et al., 2012) because recently mated females show a refractory period, due to proteins transferred by males during copulation (Chapman, Neubaum, Wolfner, & Partridge, 2000; Fricke, Wigby, Hobbs, & Chapman, 2008; Wigby & Chapman, 2005), and actively reject male mating attempts (Barnes, Wigby, Boone, Partridge, & Chapman, 2008; Van Vianen & Bijlsma, 1993). This makes individual-based copying unlikely as it would generate high rejection rates or increase sperm competition risks, except in the case of a last male advantage (Parker & Pizzari, 2010; Parker, 1970; Price, Dyer, & Coyne, 1999). In this context, developing a preference for a specific phenotype (trait-based copying, Bowers et al., 2012) rather than for a specific individual would considerably diminish the risks of sperm competition (Parker & Pizzari, 2010). A trait-based copying strategy would lead males to quickly learn to prefer a given phenotype, thus saving time and energy. This would be particularly true if males can recognize and avoid recently mated females. We know that females can visually distinguish two males of the same colour and avoid those they have recently seen mating (Loyau et al., 2012). Although we do not know whether the converse is true, it seems reasonable that males can also visually distinguish an individual female they just saw copulating from other females of the same phenotype. Alternatively, males might choose the female of the colour they did not see copulating to avoid mating with a recently mated female. This result would imply that males confounded the mated demonstrator female with the test female of the same colour, which would suggest that males use the colour of the female for individual recognition to avoid rejection and sperm competition. Alternatively, males may not copy the mate choice of others, in which case they should mate randomly, ignoring any source of social information. Based on this reasoning, we explored the existence of male mate copying in *D. melanogaster*.

METHODS

Fly Maintenance and General Procedures

We used the common laboratory Canton-S strain of *D. melanogaster*. Flies were raised in 30 ml vials containing 8 ml of a standard corn meal–agar–yeast medium at 25 ± 1 °C and $60 \pm 5\%$ humidity with a 12:12 h light:dark cycle.

Flies were sexed and sorted without anaesthesia by gentle aspiration within 6 h after emergence and kept in unisex groups of seven individuals per vial before experiments. All adult experimental flies were virgin and 3 or 4 days old after emergence. Experiments were conducted under the same conditions as the breeding (12 h daylight, 25 ± 1 °C, $60 \pm 5\%$ relative humidity). We created two artificial female phenotypes by randomly dusting females with green or pink powders (Mery et al., 2009), which created two contrasting phenotypes independent of any genetic variation. All flies were used only once as recently mated females reject further copulations for several hours (Barnes et al., 2008; Van Vianen & Bijlsma, 1993).

All experiments took place in double plastic tubes separated by a thin glass partition in the informed experimental treatment or opaque white cardboard in the uninformed treatment (control as this prevented observer females from gathering any visual information during the demonstration phase). Each mate-copying

Download English Version:

<https://daneshyari.com/en/article/8488465>

Download Persian Version:

<https://daneshyari.com/article/8488465>

[Daneshyari.com](https://daneshyari.com)