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Drosophila mate copying correlates with atmospheric pressure in a speed learning situation

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Mate choice can strongly affect fitness in sexually reproducing organisms. A form of mate choice is mate copying, in which individuals use information about potential mates by copying the mate choice of other individuals. While many studies have documented mate copying, little is known about the effect of environmental conditions on this behaviour. Here, we report the first evidence that *Drosophila melanogaster* females can acquire a sexual preference for one male characteristic after witnessing a single mate choice event (i.e. speed learning). We also found that mate copying was correlated with air pressure and air pressure changes, so that females copied far more when air pressure was high and increasing, i.e. in good and improving weather conditions. These results reveal a quick social observational learning and highlight the potential importance of meteorological conditions for mate copying, a trait potentially driving reproductive isolation.

Mate choice has important fitness consequences as it is a major driver of sexual selection (Verzijden et al., 2012). To select a suitable mate, individuals need to assess potential partners by collecting information about them. Such information can be acquired either by trial-and-error tactics or innate rules, i.e. using private information, or by monitoring other individuals with similar requirements, i.e. using inadvertent social information (Danchin, Giraldeau, Valone, & Wagner, 2004; Danchin & Wagner, 2010). In particular, the mating performance of potential mates provides public information on their quality (Nordell & Valone, 1998), and females of many species develop mating preferences that are affected by such public information (Westneat, Walters, McCarthy, Hatch, & Hein, 2000). This behaviour is called mate choice copying or more simply mate copying.

In their simplest form, mate copying experimental designs encompass two sequential phases: a demonstration followed by a test. During the demonstration, a naïve female (called the observer female) is allowed to witness two males with contrasting phenotypes, only one being chosen for copulation by another female (called the demonstrator female). During the preference test, the observer female preference is assessed by either the relative amount of time she spends near the two males or actual copulation with one of them. By copying the mate choice of others, females can also generalize their preference for any other male with similar traits (Bowers, Place, Todd, Penke, & Asendorpf, 2012), implying that mating preference may be transferred socially between individuals within populations (horizontal transmission) and across generations (vertical transmission; Bowers et al., 2012; Danchin et al., 2004).

Mate copying has been mainly reported in vertebrates (see Galef & White, 2000; Vakirtzis, 2011 for reviews) and, to our knowledge, only two studies have investigated its occurrence in invertebrates, both of them on *Drosophila*. Mery et al. (2009) provided evidence of mate copying in *Drosophila melanogaster*. In this study, the design

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differed from those used in vertebrates: the observer female witnessed not an actual choice between two males, but instead the behaviour of six females sequentially mating with one male phenotype and rejecting the other (Fig. 1). By contrast, Auld, Punzalan, Godin, and Rundle (2009) found no evidence of mate copying in *Drosophila serrata*. These contrasting outcomes may result from the difference between the experimental protocols as well as the species used. In addition, external parameters may impact copying and mating behaviours. For example, in guppy, *Poecilia reticulata*, mating behaviour is correlated with both the quantity and the spectral composition of the lighting conditions (Archard, Cuthill, & Partridge, 2009). In insects, mating behaviour has been shown to be impacted by atmospheric pressure (Ankney, 1984; Austin, Guglielmo, & Moehring, 2014; McFarlane, Rafter, Booth, & Walter, 2015; Pellegrino et al., 2013).

Here, we investigated whether *D. melanogaster* females can acquire a sexual preference for one male characteristic after witnessing a single mate choice event. We also examined the effects of external parameters, especially air pressure, on mate copying. We had long noticed that the extent of mate copying seemed to be correlated with weather conditions during the experiment. As we controlled temperature, light and humidity, we postulated that the main external parameter potentially explaining a weather effect should involve air pressure. This seemed coherent with the fact that a change in weather, in particular the arrival of heavy rains or storms, can have serious fitness consequences for small animals such as insects (Wellington, 1946) but can also be relatively well predicted by monitoring air pressure. Good weather is usually associated with high air pressure, whereas rain mostly happens in low air pressure conditions (Ahrens, 2009). Air pressure change also needs to be considered: a rapid drop indicates an approaching storm or heavy winds (Ahrens, 2009). Even though the influence of weather on animal behaviour has been observed by humans for centuries (Aristotle, trans. 1883, e.g. XXVII:46), it has been investigated only in a few studies in mammals (Paige, 1995), birds (Breuner, Sprague, Patterson, & Woods, 2013; Metcalfe, Schmidt, Bezner Kerr, Guglielmo, & MacDougall-Shackleton, 2013), fish (Heupel, Simpfendorfer, & Hueter, 2003) and insects (Ankney, 1984; Austin et al., 2014; McFarlane et al., 2015; Pellegrino et al., 2013). In particular, mating behaviour has been shown to be affected by air pressure changes in the cucurbit beetle, *Diabrotica speciosa*, the true armyworm moth, *Pseudaletia unipuncta*, and the potato aphid, *Macrosiphum euphorbiae* (Pellegrino et al., 2013). In *D. melanogaster*, only two studies have focused on the influence of air pressure on the prevalence of sexual behaviour (Ankney, 1984; Austin et al., 2014). Ankney (1984) found that *Drosophila* mating frequency decreases in low air pressure conditions. Austin et al. (2014) found an effect of air pressure change on *D. melanogaster* courtship and mating frequency: in decreasing air pressure some flies showed reduced mating activity, whereas others increased it. But the effects of air pressure on other aspects of sexual behaviour such as mate choice or, more generally, on cognitive abilities, have never been investigated.

Here, we report the results of two experiments followed by a correlational analysis of the potential role of air pressure on fruit fly sexual behaviour. Experiment 1 investigated whether *Drosophila* females can perform mate copying in a protocol similar to those traditionally used in studies of mate copying in vertebrates. To this aim, we performed and compared two experimental designs of mate copying. The first design (adapted from Mery et al., 2009) involved six apparent female choices in a sequence (long demonstration protocol, Fig. 1). The second design involved a single live demonstration of one female choosing between two males of contrasting phenotypes (short demonstration protocol, Fig. 1). Very little is known about the ecology of *Drosophila* in the wild (Reaume & Sokolowski, 2006), and it is uncertain whether *Drosophila* females have the opportunity to experience sequential demonstrations of mate choice in nature as in the long demonstration protocol. Thus, in addition to bridging the gap with vertebrate studies, the rationale for our short demonstration protocol was that if *Drosophila* females were able to perform mate copying in speed learning situations, then our confidence that they can perform mate copying in nature would be greatly increased. The short demonstration protocol thus tested whether young virgin females can acquire a preference for a given male phenotype after the observation of one female choosing and copulating with one of two

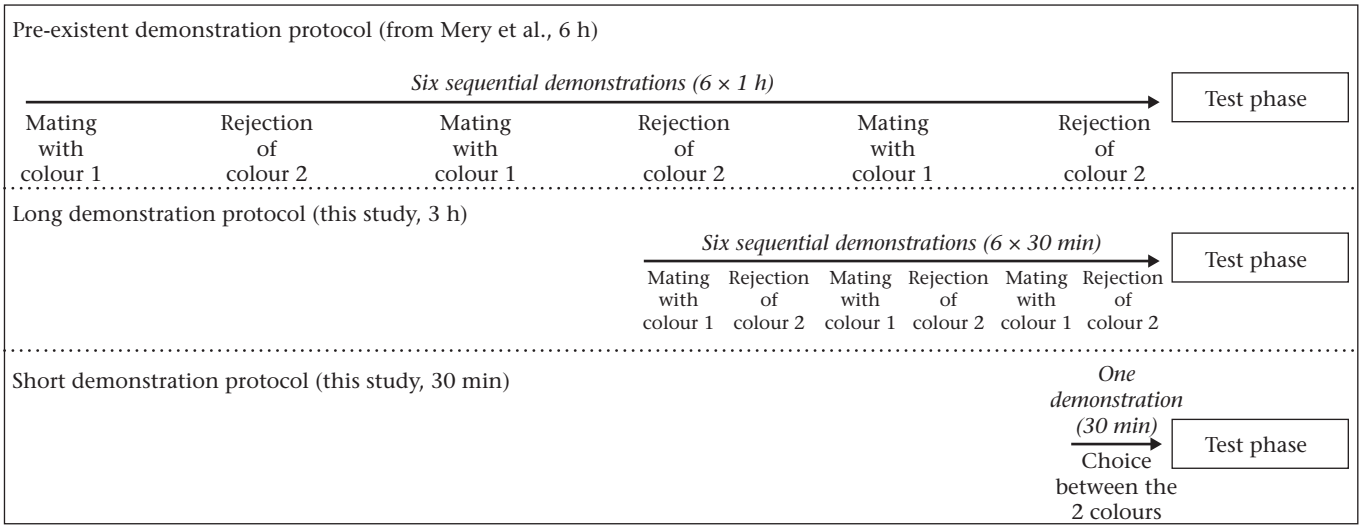

Figure 1. *Drosophila* mate copying protocols: the first was used in the second experiment of Mery et al. (2009); the other two were used in this study. Our long demonstration protocol followed that of Mery et al., except that each demonstration step lasted for 30 min instead of 1 h. Both consisted of a sequence of demonstrations involving one virgin female mating with a male of one colour, followed by a demonstration with a recently mated female rejecting the male of the other colour. These two steps were repeated three times for a total of 6 h in Mery et al.'s study versus 3 h in our long design. The short demonstration protocol involved only one live demonstration of one female freely choosing between two differently coloured males (experiment 1), or a female already copulating with a male of one colour plus a male of the opposite colour next to them (experiment 2). This shorter demonstration phase lasted 30 min. In both protocols, the preference test was run just after the demonstration and the colour of the male with which the observer female copulated was recorded and used to estimate its preference.