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Exposure time to rivals and sensory cues affect how quickly males respond to changes in sperm competition threat

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Phenotypic plasticity can increase fitness in rapidly changeable environments, but may be limited if the underlying mechanisms cause a lag between environmental change and individual response or if the information individuals receive is unreliable. Hence to understand the evolution of plasticity we need to assess whether individuals respond to fine-scale variation in environmental cues. In this study we used a *Drosophila melanogaster* fruit fly model to investigate factors that determine how quickly males alter their behaviour in response to changes in sperm competition cues. Male *D. melanogaster* respond to exposure to rival males prior to mating by extending mating duration and increasing ejaculate investment. We have previously shown that to build-up the response, males need about 24 h exposure to a rival. We reasoned that this time lag was necessary to increase ejaculate production, but this physiological limitation should not apply when moving from high- to low-competition environments; hence we predicted that males should immediately decrease their investment when competition is removed. Here we tested this by measuring how long rival-exposed males maintained an extended mating duration after removal of the rival. We assessed how exposure time and sensory information affected the speed of change in behavioural state. Males maintained extended mating duration for hours after a rival was removed, but this was dependent on time of exposure to a rival. Furthermore, although sensory-impaired males were able to respond to rivals, the time required for the response to build and diminish depended on males possessing their full sensory repertoire. Our results suggest that males use exposure time and multiple sensory cues to assess whether the threat of sperm competition is transient (so unlikely to translate into realized competition) or sustained (requiring a response). Therefore, time lags between environmental changes and responses may buffer animals against making hasty decisions in fluctuating environments.

Phenotypic plasticity is the expression of different phenotypes from the same genotype in response to an environmental cue (West-Eberhard, 2003). In animals, behavioural plasticity is predicted to be a particularly potent form of phenotypic plasticity due to its rapid flexibility and low production costs (Parker, 1982), and hence flexible behaviour can enable animals to cope with fluctuating environments (Komers, 1997). However, to be adaptive, behavioural plasticity must track the environment accurately and on a similar timescale to the environmental variation to which it responds (Gabriel, Luttbeg, Sih, & Tollrian, 2005). If it does not, mismatches between behaviour and the environment are predicted to be costly (Auld, Agrawal, & Relyea, 2010). For example, there is growing evidence that climate change is currently driving phenological mismatches in reproduction (Reale, McAdam, Boutin, & Berteaux, 2003), development of seasonal camouflage (Mills et al., 2013), hibernation emergence (Lane, Kruuk, Charmantier, Murie, & Dobson, 2012; Ozgul et al., 2010) and migration (Both & Visser, 2001). Clearly, gaining accurate information in order to predict future environments is essential, and this requires sensory systems that can assimilate environmental information. Moreover, depending on the type of environmental variation, the proximate cues might change more quickly than the prevailing population conditions, and so animals might need to judge whether the change is transient or sustained enough to warrant a response. We therefore need to assess whether individuals respond to fine-scale variation in environmental cues.

One rapidly changing facet of the environment is the sociosexual context, as sex ratio can vary locally and over short timescales (Kasumovic, Bruce, Andrade, & Herberstein, 2008; Punzalan, Rodd,

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& Rowe, 2010). This is particularly important for males as they are predicted to allocate reproductive resources strategically, trading off current and future mating opportunities depending on the competitive environment (Parker, Ball, Stockley, & Gage, 1996, 1997). Plastic mating strategies in response to changing sociosexual environments are well documented, with males strategically allocating ejaculates (Wedell, Gage, & Parker, 2002) and/or adjusting behaviour (Bretman, Gage, & Chapman, 2011). Some of these strategies are an immediate response to another male (or cues of other males) present at the time of mating; others require a period of exposure to a rival beforehand, although few studies are designed to measure both (Bretman, Gage, et al., 2011). We currently have very little understanding of how males assess and assimilate environmental information and how this is translated into altered behavioural and physiological states. One of the best studied examples is the response of male *Drosophila melanogaster* fruit flies, whereby males exposed to a rival male before mating subsequently mate for longer than males held alone (Bretman, Fricke, & Chapman, 2009). This leads to increased short-term reproductive success compared to males that have not been exposed to rivals (Bretman et al., 2009), mediated by alterations in ejaculate contents (Garbaczewska, Billeter, & Levine, 2013; Moatt, Dytham and Thom 2014; Wigby et al., 2009). Individual males can alter mating duration in either direction, increasing it after exposure to a rival and reducing it when that rival is removed (Bretman, Westmancoat, Gage, & Chapman, 2012). Males kept with rivals die sooner and become progressively less successful at obtaining matings over their lifetimes, supporting the idea that there are costs of responding to rivals (Bretman, Westmancoat, Gage, & Chapman, 2013). Males detect rivals via any paired combination of olfactory, auditory and tactile sensory cues, which implies a system of sensory redundancy and reinforces the idea that making the wrong decision about the appropriate level of investment is costly (Bretman, Westmancoat, Gage, & Chapman, 2011).

In this study, we explored how quickly males respond to a new competitive environment and what factors affect the speed of adjustment. We have previously shown that males require about 24 h exposure to a rival to increase mating duration and gain fitness benefits, and we reasoned this time lag may be required to increase production of ejaculate components (Bretman, Fricke, Hetherington, Stone, & Chapman, 2010). However, males moving from a high- to a low-competition environment should not be constrained by this physiological limitation and so should not require any adjustment time. If this is the only consideration in the speed of response, then we predict that males moved from high to low competition should quickly change their strategy and not mate for longer than males that have never perceived competition. We measured how long rival-exposed males continued to extend mating duration after the rival had been removed and how this was affected by the length of exposure time. We also tested how sensory information affected the speed of response to changes in the sperm competition environment by manipulating auditory and olfactory inputs.

METHODS

Experiments were conducted in a 25 °C humidified room with a 12:12 h light:dark cycle, using plastic vials (75 × 25 mm) with 7 ml standard sugar–yeast–agar medium (Bass et al., 2007). All wild-type flies were the Dahomey strain as in our previous studies. Larvae were raised at a standard density of 100 per vial. At eclosion, flies were collected and sexed using ice anaesthesia, and stored 10 per vial. Females were supplemented with live yeast granules. Males were aged for 24 h before being randomly assigned to a social environment treatment, i.e. plus-rival or no-rival, with a starting $N = 40$ for all groups. In different experiments we manipulated 'exposure time' (time from introduction to removal of the rival) and 'maintenance time' (time from removal of the rival to mating; Fig. 1, Table 1). At mating, males were aspirated singly into a vial containing a single female and allowed to mate, and mating duration was recorded. If no mating occurred within 2 h the vial

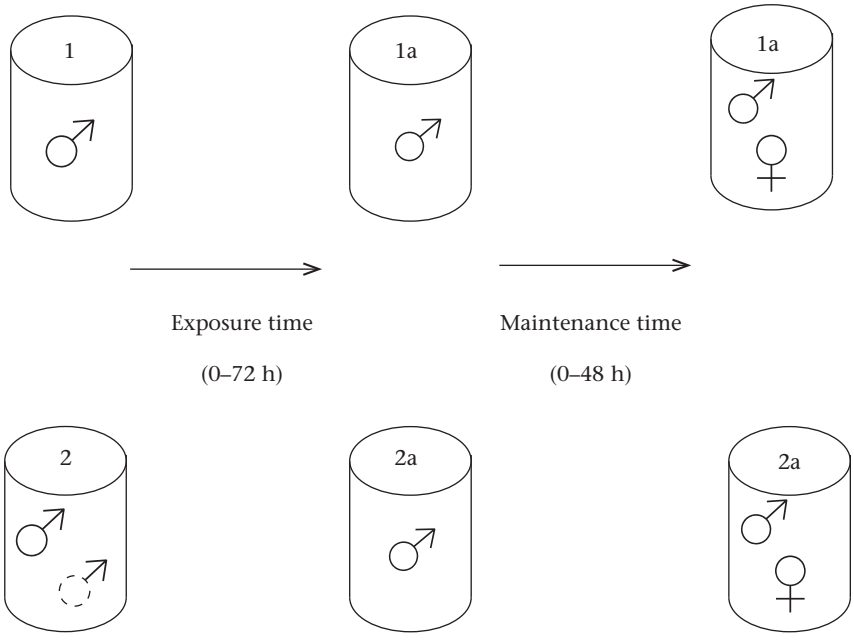

Figure 1. Experimental design. Focal males (solid symbols) were separated at eclosion and haphazardly assigned to no-rival (vials 1) or plus-rival (vial 2, rival is the dotted symbol) treatments, handled in exactly the same way except for the presence of absence of the rival. In different experiments we varied exposure time (time kept with the rival male) and maintenance time (time from removal of the rival male until mating), as described in Table 1. Focal males were transferred to new vials for isolation (vials 1a and 2a) and females were added to these vials to record mating duration.