



## Diet alters *Drosophila melanogaster* mate preference and attractiveness



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### ARTICLE INFO

#### Article history:

Received 23 March 2016  
Initial acceptance 17 May 2016  
Final acceptance 19 September 2016

MS. number: A16-00266R

#### Keywords:

attractiveness  
behaviour  
diet  
*Drosophila*  
fitness  
mate choice  
preference  
reproduction

Animals decide which potential mate to pair with based on their subjective evaluation of each candidate mate's attractiveness. Attractiveness and its perception are plastic traits, dependent upon genetic and environmental factors. When evaluating mate attractiveness, in some cases animals make predictive judgements of mate reproductive potential, or fitness, based on the mate's condition. Diet, a fluctuating environmental factor, influences health and conditional states. However, how dietary enrichment of individual macronutrients (fat, protein or sugar) affects behaviour, mate choice and reproductive outcomes in both sexes is not fully understood. Here we show that a moderate increase in dietary macronutrients alters attractiveness, mate preference and reproductive output of *Drosophila melanogaster*. Our results demonstrate that diet is an important factor in determining mating behaviour and reproductive output, acting in a sex-specific fashion. These findings provide a framework for exploring the genetic mechanisms that drive changes in mating behaviour, fitness and, hence, trait evolution.

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How and why an animal selects a particular mate from among a pool of potential mates is a complex and incompletely understood process that is influenced by the continuously changing environment in which animals live. Animals evolve preferences for certain traits; these preferences fall along a continuum and are influenced by the animal's own condition and genetic make-up (Holbeck & Riebel, 2009; Hunt, Brooks, & Jennions, 2005; Lopez, 1999; Penton-Voak et al., 2003; Rodríguez & Greenfield, 2003). Sexual selection theory posits that the most attractive animals gain the largest number of matings and produce the most offspring (Andersson & Simmons, 2006; Jones & Ratterman, 2009). Mate preference can affect allelic distributions in populations via assortative mating that creates barriers to gene flow and is therefore an important force driving evolution and speciation (Arnegard et al., 2010; Mullen, Mendelson, Schal, & Shaw, 2007; Nosil, Crespi, Gries, & Gries, 2007; Shaw & Lesnick, 2009; Turner & Burrows, 1995). Consequently, understanding how fluctuating environmental factors shape mate preferences is integral to understanding species maintenance and hybrid avoidance (Miller & Svensson, 2014). While females are considered the 'choosy' sex in most cases, males also play a role in determining whether or not a mating

occurs (Amundsen & Forsgren, 2001; Edward & Chapman, 2011, 2012, 2013), further complicating the study of mate choice.

Mate preference, which is the attraction of an animal to another with particular phenotypic characteristics, underlies mate choice and is a condition-dependent trait, meaning that discrimination between potential mates depends upon the internal physiology of the choosing animal (references above and reviewed by Cotton, Small, & Pomiankowski, 2006). Therefore, preferences measured in a static scenario may not always predict mating outcomes as the 'preferred' partner could change depending upon a variety of environmental constraints such as access to mates of differing quality and availability of resources (Borgia, 1980; Chaine & Lyon, 2008; Danielson-Francois, Kelly, & Greenfield, 2006; reviewed by: Miller & Svensson, 2014; Svensson & Waller, 2013). However, high-condition animals, those with greater reproductive potential resulting from increased available energy stores, are generally more choosy when picking mates, are preferred by high-quality mates, gain greater numbers of matings and are more fecund (Bakker, Künzler, & Mazzi, 1999; Hebets, Wesson, & Shamble, 2008; Hingle, Fowler, & Pomiankowski, 2001; Hunt et al., 2005; Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Lerch, Rat-Fischer, Gratier, & Nagle, 2011; Lerch, Rat-Fischer, & Nagle, 2013; Mazzi, 2004; Møller, 1991; Moore & Moore, 2001; Petrie, 1983; Rintamäki, Alatalo, Höglund, & Lundberg, 1995; Rintamäki, Lundberg, Alatalo, & Höglund, 1998). While mate choice has the potential to confer fitness benefits in terms of offspring quantity or

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quality (Bos, Williams, Gopurenko, Bulut, & Dewoody, 2009; Byrne & Rice, 2006), mate discrimination is costly. Energy is spent on increased sampling of the population and fending off courtship advances from undesirable mates, and poor-condition individuals are expected to exhibit lower levels of discrimination because the benefits gained from mate discrimination do not outweigh the costs (Cockburn, Osmond, & Double, 2008; Cotton et al., 2006; Hingle et al., 2001; Holveck & Riebel, 2009; Wilgers & Hebets, 2012), resulting in increased rates of pairing between poor-condition individuals (Janicke, David, & Chapuis, 2015; Kunz & Uhl, 2015; Xue et al., 2016). Alternatively, if the benefits gained from mating with good-condition animals continue to outweigh the costs of choosiness, poor-condition animals would be expected to continue to prefer good-condition mates, and evidence exists to support this hypothesis (Griggio & Hoi, 2010; Perry & Rowe, 2010).

Unstable environments can lead to fluctuating mate preferences, so it is important to understand how continually changing environmental factors, such as nutrient availability, influence mate choice (reviewed by Miller & Svensson, 2014). Animal fitness is dependent upon condition and can be influenced by environmental factors such as diet, and nutrient availability has been shown to affect sexual selection and mate choice (Janicke et al., 2015; Kunz & Uhl, 2015; Xue et al., 2016). The best ratio of macronutrients (fat, protein and sugar) varies by sex and species, but an ideal diet increases lifetime fecundity (Lee et al., 2008; Maklakov et al., 2009; Pirk, Boodhoo, Human, & Nicolson, 2010; Solon-Biet et al., 2015). If imbalanced diets decrease fecundity, we expect that good-condition animals will find these mates less attractive and will modify their behaviour while poor-condition individuals will not.

Given the complexity and number of open questions surrounding mate choice, disentangling these variables is a vexing problem. However, the genetically tractable *Drosophila melanogaster* provides a good animal model for assessing how diet affects mate preference and individual attractiveness. Fruit fly mating behaviour has been intensively studied and described, as have the underlying required genetic and neural circuits (reviewed by Yamamoto & Koganezawa, 2013). *Drosophila melanogaster* mate preference has been shown to have a genetic basis, as female preferences for male genotype vary by inbred line, while male preference rankings of female genotypes are largely independent of male genotype (Ratterman, Rosenthal, Carney, & Jones, 2014). *Drosophila melanogaster* mate preferences also can be altered by environmental factors such as temperature fluctuation (Narraway, Hunt, Wedell, & Hosken, 2010) and diet (Cook & Connolly, 1976; Cook & Cook, 1975; Fedina et al., 2012; Kuo et al., 2012; McRobert, 1986; Mery et al., 2009; Nandy, Joshi, Ali, Sen, & Prasad, 2012).

In the wild, *D. melanogaster* consume rotting fruit that is colonized by yeast (Broderick & Lemaitre, 2012). Fruit macronutrient content varies based on genetics, environment and season (Arvanitoyannis & Mavromatis, 2009), and as yeast contains protein and lipids, the extent of colonization will also contribute to dietary diversity in a natural landscape. As adult *D. melanogaster* have wide dispersal ability (Coyne et al., 1982), sexually mature adults that have developed on substrates of varying quality likely aggregate and mate on new food sources. In this scenario, condition-dependent discrimination of mates of varying quality could be important for maximizing fitness. While a link between diet and attractiveness has been demonstrated in *D. melanogaster*, a thorough understanding of how specific macronutrients (fat, protein or sugar) affect mate preference is lacking and could be expanded upon by addressing gaps in previous studies. The effect of dietary fat has not yet been examined, and mate preferences have often been measured indirectly via physical separation of flies (Mery et al., 2009) or through elicitation of courtship by immobilized or decapitated females that cannot perform a full repertoire of

mating behaviours (Cook & Connolly, 1976; Cook & Cook, 1975; Fedina et al., 2012; Kuo et al., 2012; McRobert, 1986). Additionally, previous studies examined the effects of diet on one sex at a time. Our study aims to systematically characterize changes in mating behaviour and preference caused by specific increases in each individual macronutrient in intact, freely performing animals (Reed et al., 2010, 2014). We tested for dietary effects on mate preference in each sex by conducting in-depth analyses of mating behaviours and asked whether changes in behaviour corresponded with potential fitness, which we approximated with measures of fecundity for 5 days after mating. We expected that diet would alter the fecundity of the flies either positively or negatively and that we would detect changes in behaviour as a consequence.

## METHODS

### Fly Husbandry

In this study, we used Canton-S (CS) flies that had been isogenized for 10 generations via single-pair sibling matings and maintained continuously on standard laboratory diet (*Drosophila* agar, 10 g/litre; dextrose, 40 g/litre; sucrose, 20 g/litre; nutritional yeast, 12 g/litre; cornmeal, 70 g/litre; 3 ml/litre of 10% Tegosept). We placed five 5–10 day old, nonvirgin female and male CS flies in bottles containing 75 ml of either control or macronutrient-enriched food. The diets used to manipulate macronutrient content were modified from Reed et al. (2014): control (C, 7 g/litre of agar, 65 g/litre of cornmeal, 13 g/litre of inactive yeast, 7.5 g/litre of sucrose); high fat (C + 30 g/litre of coconut oil); high protein (C + 30 g/litre of sodium caseinate); and high sugar (C with 40 g/litre of total sucrose). We used Tegosept as a preservative in all diets. The control diet is similar to diets used in many *D. melanogaster* studies, including in our laboratory. In the enriched diets, each macronutrient was increased by approximately 3%.

After 5 days, we removed the parents and collected progeny upon eclosion beginning at 1 h after 'lights on' within a 3 h window. Progeny matured in vials containing their respective diet for 5 days, with females in groups of five and males in isolation. We housed males in isolation to minimize the effect of perceived competition, which is known to alter male reproductive behaviours (Bretman, Fricke, & Chapman, 2009). We know of no effect on mating behaviours of aging females in groups, and it is standard laboratory practice to do so (Ejima & Griffith, 2007). We raised all flies in the study in an incubator at 25 °C with a 12:12 h light:dark cycle. We performed all behavioural experiments on 5-day-old flies and did not anaesthetize flies on experimental days. Flies mated in 1 cm diameter and 0.785 cm<sup>3</sup> Plexiglas chambers containing moistened filter paper. We recorded fly interactions using JVC-HDD Everio and Sony HD Handycam cameras and stopped recording after mating was complete.

### Single-pair Mating Assay

To evaluate how diet affects mate preference, we first used single-pair mating assays in which one male and one female were placed together in a courtship chamber and scored for various behavioural parameters. These assays are often referred to as 'no-choice' assays, although animals have a choice between mating and not mating. However, most flies mate during the assay period, and we evaluate their overall preferences using the parameters described below. Single-pair mating assays are ideal for determining preferences without the experimental confound of intra-sexual competition. In our experiments, we quantified mating behaviours of animals raised on the control diet that were paired with individuals raised on either the control diet or on each of the

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