

Life history variation in male mate choice in *Drosophila melanogaster*

Dominic A. Edward*, Tracey Chapman

School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, U.K.

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Variation in life history arises when individuals adopt alternative strategies for allocating finite resources to different traits to maximize fitness. Optimal strategies can vary not only between, but also within, species, and in particular between males and females. Variation in life histories can therefore affect the relative importance and impact of sexual selection, and this will itself feed back into how life histories evolve. Previous work has revealed that female mate choice tends to decline with age. However, similar measures of life history variation in male mate choice are lacking. We addressed this in an investigation of male mate choice in *Drosophila melanogaster*. We gave males the opportunity to choose a mate every day of their lives then measured variation in reproductive output. Males that were given the opportunity to choose their mates showed a subtle but significant benefit of choice during their early reproductive lives. This was negated during their late reproductive lives, however, when it was males that were given a randomly selected mate each day that fared progressively better in terms of number of offspring gained. This evidence suggests that a life history trade-off between early and late reproduction can arise in males given a regular choice of mate. We therefore identified novel age-dependent variation in the benefits of male mate choice. Our study shows the importance of considering choice in the context of life history, to gain more accurate estimates of the fitness benefits of choice.

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Individuals of both sexes have a finite pool of resources to allocate between different traits and at different life stages. This yields a great diversity of potential life histories. Central to our understanding of the evolution of life histories is the assumption that not all traits can be maximally expressed all of the time; hence trade-offs will occur (Stearns 1989). For example, it is expected that investment of resources in current reproductive effort will trade off with the ability to reproduce in the future or with somatic maintenance (Roff 1992). Whether it is most profitable to invest in current reproduction or to conserve resources for the future will ultimately shape the evolution of life histories for each species.

Much research effort has been focused on identifying the factors that favour the expression of contrasting life histories across different species. However, there is also huge variation found within species, either as a result of different 'fixed' strategies selected in different populations or of life history plasticity. In particular, sex-specific life histories are predicted to evolve because of strong sex-specific selection pressures (Bonduriansky et al. 2008). For example, males may often allocate greater resources to

traits that enhance their ability to compete for mates, while females will often allocate greater resources to the production and care of offspring (Trivers 1972). When males invest more resources in secondary sexual traits, this can result in a life history trade-off that may, for example, reduce male ability to provide parental care (Gustafsson et al. 1995), affect immune responses (Jacot et al. 2004) and reduce male life span (Hunt et al. 2004; Punzalan et al. 2008). Thus male and female life histories are expected to differ. Sex-specific selection typically favours a male strategy of 'live fast, die young' while female life histories are characterized as being lower risk, with fitness returns spread over a relatively longer timeframe (Vinogradov 1998; Hunt et al. 2004; Bonduriansky et al. 2008).

Identifying the causes and consequences of sex-specific life histories is important for understanding the relationship between life history and sexual selection. There are two perspectives to this relationship. On the one hand, we can consider the influence that life history variation will have upon the patterns and strength of sexual selection. For example, sex differences in life history traits such as mortality can determine sex ratios that will influence the strength and direction of sexual selection (Kokko & Monaghan 2001). Also, if the expression of traits that are fundamental to sexual selection, such as mating preferences and secondary sexual traits, vary at different life stages this will ultimately have an impact upon sexual selection within a population (e.g. Kokko 1997). Consequently, measurements of sexual selection will be incorrect if

* Correspondence and present address: D. A. Edward, Mammalian Behaviour & Evolution Group, Institute of Integrative Biology, University of Liverpool, Leahurst Campus, Chester High Road, Neston CH64 7TE, U.K.

E-mail address: dedward@liv.ac.uk (D. A. Edward).

demographic factors are not considered. In addition to the effect that variation in life history can have on sexual selection, we can also consider the reverse, that is, how the intensity of sexual selection itself might influence the evolution of life histories. It has been shown that sexual selection can influence age-dependent reproductive effort and the evolution of life span and ageing, thus contributing to the evolution of sex-specific life histories (e.g. Archer *et al.* 2012). For example, if male mating success increases with age then selection can favour increased longevity (Graves 2007). In addition, when sexual selection favours the production of larger sperm, males may not reach sexual maturity until they are older (Pitnick *et al.* 1995). In summary, a complete understanding of either sexual selection or life history evolution cannot be achieved if these processes are studied in isolation. Parallel studies of either field may overlook the complex, interesting and highly biologically relevant interactions between them (Hoglund & Sheldon 1998; Badyaev & Qvarnstrom 2002; Bonduriansky *et al.* 2008).

In this study we explored the relationship between life history and sexual selection by measuring life history variation in the expression of male mate choice. Previous studies on this general topic are overwhelmingly biased towards reporting variation in female, rather than male, preferences. In the majority of cases the strength of female mate choice has been found to decline with increasing age, for example in cockroaches, *Nauphoeta cinerea* (Moore & Moore 2001), Mediterranean fruit flies, *Ceratitis capitata* (Anjos-Duarte *et al.* 2011), house crickets, *Acheta domesticus* (Mautz & Sakaluk 2008), wolf spiders, *Schizocosa ocreata* (Uetz & Norton 2007; Wilgers & Hebets 2012) and guppies, *Poecilia reticulata* (Kodric-Brown & Nicoletto 2001). However, there are contrasting examples in which age had no effect on female mate choice, such as in field crickets, *Gryllus pennsylvanicus* (Judge *et al.* 2010). A principal explanation for the widely reported age-dependent decline in female choosiness is that mate choice is predicted to be a condition-dependent trait (e.g. Hunt *et al.* 2005; Cotton *et al.* 2006), and negative correlations between age and condition are frequently reported (Moore & Moore 2001). In terms of life history trade-offs, as females age and the pool of available resources diminishes, fitness payoffs may be greater if remaining resources are allocated directly to reproduction instead of mate choice. Another potential explanation for the age-dependent decline in female choosiness is that as female mortality increases this will favour allocation of resources to current reproductive effort (e.g. Creighton *et al.* 2009). Mate choice may then be detrimental to fitness, as the rejection of any potential mates could delay reproduction.

Although a typical pattern is emerging that female choosiness declines with age, it is unclear whether this is typical of mate choice in general or a sex-specific pattern. The prevalence and significance of male mate choice is now increasingly recognized (Edward & Chapman 2011) yet age-specific variation in male mate choice has scarcely been considered. Although choosiness tends to decline as females get older, it does not follow that this should be the case for males, particularly if sex-specific life histories are the norm (Vinogradov 1998). However, only one previous study in the parasitoid *Trichogramma turkestanica* measured, but found no evidence for, age-dependent variation in male mate choice (Martel *et al.* 2008).

The principal explanations for a decline in female mate choice, that is, condition dependence and increased investment in current reproduction (see above), could also apply to males. However, there are also reasons why male choosiness may not decline with age, or may not decline as fast, relative to the rate in females. If male life histories are generally predicted to follow a 'live fast, die young' pattern distinct from that favoured in females, then this may select against male mate choice at a young age. This is because young males will have the ability to express a high mating rate, and thus

would not benefit from rejecting any potential mates. If males are under strong selection to accept all mates, this will prevent the expression of choice. Related to this, male ability to express choice is frequently limited by the number of potential mates available relative to a male's resources to mate (Edward & Chapman 2011). However, older males can sometimes be preferred by females if age is an indicator of 'good genes' (Kokko 1998) and if older males invest more resources in each mating (Avent *et al.* 2008). Consequently older males may attract a greater number of potential mates than younger males, which, combined with a reduced ability to mate as males get older, would select for increased mate rejection and thus the opportunity to express choice.

Thus, male mate choice could decline with age as is commonly observed in females or the pattern could be different for males because of sex-specific selection pressures that influence life histories. As there is little empirical and no formal theoretical consideration of sex-specific variation in mate choice it is difficult to formulate clear predictions for how male mate choice will vary with age and whether typical patterns of variation should be expected. We therefore addressed this question directly by measuring life history variation in male mate choice in the fruit fly, *Drosophila melanogaster*.

Male *Drosophila* exhibit mate choice, typically preferring larger and more fecund females (Gowaty *et al.* 2002, 2003; Byrne & Rice 2006; Long *et al.* 2009; Edward & Chapman 2012). In our study, male *D. melanogaster* were assigned to one of two treatment groups: half were given the opportunity to choose a mate and half were not. Males given a choice could choose between two females each day for their entire lives. Males not given a choice were given a single, randomly selected female each day. For all males we measured life span and daily age-specific reproductive success until death. This study is therefore the first, to our knowledge, to investigate age-dependent variation in male mate choice in *D. melanogaster* and the first to detail the daily fitness consequences of mate choice during the entire life span of any organism. It is expected that males will express a preference for more fecund females at a young age, as this behaviour has previously been recorded in the same stock population using a similar experimental design (Edward & Chapman 2012). The purpose of this study was to determine whether this preference persisted throughout the male life span.

METHODS

Experimental Procedure

Flies were obtained from the Dahomey stock, which is a large outbred laboratory population with overlapping generations. This stock has adapted to the laboratory environment over hundreds of generations; hence it can be considered a laboratory island population ideally suited to this kind of study (Rice *et al.* 2006). Furthermore, as no direct selection is imposed upon life span during routine husbandry of this stock, the measure of life span provides information relevant to variation in individual fitness. All culture and experimental conditions were performed at 25 °C and a 12:12 h light:dark cycle. Vials (75 mm height and 25 mm diameter) each containing 8 ml of standard sugar–yeast food (100 g brewer's yeast, 100 g sucrose, 20 g agar, 30 ml Nipagin (10% w/v solution) and 3 ml propionic acid per 1 litre of medium) were used throughout. Larval density within the stock culture varies; hence all flies were reared at a density of 100 larvae per vial to minimize variation between females used on different days. Previous results have shown that, when flies are reared under these conditions, there is sufficient variation in female fecundity for males to distinguish potential fitness benefits (Edward & Chapman 2012). All

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