

Learning in the context of sexual behaviour in insects

REUVEN DUKAS*

*Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour,
McMaster University, 1280 Main Street West Hamilton, Ontario, L8S 4K1, Canada*

Abstract—There has been little ecological and evolutionary research on learning in the context of sexual behaviour in insects. The traditional views still dominating the literature are that insects are short-lived and have little opportunity to learn about courtship and mating. In this paper I challenge these views by illustrating, theoretically, that at least some insects have ample opportunities to learn in the context of sexual behaviour and that such learning may be beneficial. Some of the best empirical evidence for learning about sexual behaviour in insects is reviewed and future directions in this fruitful area of research are suggested. The role of learning in insect sexual behaviour has probably been underestimated. Such learning may have had an important effect on sexual selection and incipient speciation.

Keywords: courtship; *Drosophila*; fruit flies; learning; mate choice; speciation.

INTRODUCTION

Research in the past few decades has demonstrated that many insect species rely heavily on learning to decide about a variety of behaviours, including diet choice, predator avoidance, spatial orientation and social interactions (Alloway, 1972; Papaj and Prokopy, 1989; Papaj and Lewis, 1993; Dukas, 2001; Greenspan and van Swinderen, 2004). The role of learning in insect sexual behaviour, however, has been either neglected or considered negligible by evolutionary and behavioural ecologists (Alexander et al., 1997). It is easy to understand why little attention has been devoted to learning in the context of courtship and mating in insects. First, in many insects, the males appear to be rather indiscriminate and the females mate only once (Alexander et al., 1997). Either of these features would make learning in the context of sexual behaviour less likely to evolve. Second, the prime model system for insect learning has been social bees, in which workers are asexual (Heinrich et

*E-mail: dukas@mcmaster.ca

al., 1977; Lavery and Plowright, 1988; Menzel and Muller, 1996; Giurfa, 2003). This has diminished the opportunity for extensive research on the effect of learning on sexual behaviour.

The scarcity of ecological and evolutionary research on learning in the context of sexual behaviour in insects is probably not well justified. First, we know relatively little about learning in relation to courtship and mate choice, even in vertebrates. Work on that topic in insects can help us to generate better general knowledge on the evolutionary biology of learning in relation to sexual behaviour. Insects are especially suited for such research because they are readily available in large quantities and have a short lifespan. Second, learning is involved in processes determining sexual selection and incipient speciation (Gibson and Langen, 1996; Irwin and Price, 1999; ten Cate and Vos, 1999; Beltman et al., 2004; Lachlan and Servedio, 2004) and many research programmes on these processes have used insects as model systems (Coyne and Orr, 1989, 2004; Rice and Hostert, 1993; Andersson, 1994). Hence, quantifying the effects of learning on sexual behaviour in male and female insects can help us understand sexual selection and incipient speciation.

My review has three parts. In the first part, relevant published theory and further ideas on the likelihood of learning in the context of courtship and mating behaviour in insects are discussed. The second part concentrates on some of the best evidence for learning in the context of sexual behaviour in insects. Finally, the third part outlines promising avenues for further research in this area. The review will focus on selected examples from fruit flies (*Drosophila* spp). Such a focus is well justified because fruit flies have served as a central model system in both evolutionary and mechanistic research on sexual behaviour (Spieth, 1974; Hall, 1994; Greenspan and Ferveur, 2000).

THEORY

Critique of current theory

There has been little discussion of the optimal investment in learning in the context of mating behaviour in any species. Ernst Mayr (1974, p. 652) eloquently summarised the prevailing sentiments about learning in the context of sexual behaviour in insects by stating that "In many species, particularly short-lived ones, mating may occur only a single time in the whole life of an individual, often within hours after metamorphosis or emergence from the pupa. . . There is no opportunity whatsoever for learning through experience." Roitberg et al. (1993) elaborated on Mayr's idea with a model evaluating the value of learning in the context of mate choice in insects. They concluded that occurrences of learning in the context of mate choice would be less common than learning in the context of other behaviours, such as prey choice. Similarly, Alexander et al. (1997) argued that learning in the context of mate choice in insects is unimportant because insects have a short lifespan and

may not have the opportunity to learn about potential mates. For example, young mammals and birds typically interact with their parents for extended periods. This parent-offspring contact allows immature individuals to learn about various traits they can later seek in prospective mates. Most insects, however, do not interact with their parents; hence, they lack opportunities for learning about such traits.

The published ideas about learning in the context of sexual behaviour in insects are intriguing but unconvincing. Theoretically, the value of learning depends on its net effect on fitness, which may be positive even in short-lived species (Dukas and Visscher, 1994; Dukas, 1998). Furthermore, two features of the model of Roitberg et al. (1993) were probably responsible for underestimating the value of learning in the context of mate choice. Roitberg et al. (1993) compared learning by female parasitoid insects within two central fitness contexts, host seeking and mate choice. In the model, non-learning individuals were allowed to use information about the a priori distribution of mate quality whereas learning individuals relied solely on their experience. As a result of this assumption, the fitness of learning individuals with a memory window of one time period was much lower than that of non-learners. A more realistic assumption would be to allow learners to elaborate on innate knowledge. Second, Roitberg et al. (1993) assumed that a major difference between host and mate seekers is the number of events contributing to experience, with the events being numerous eggs laid versus very few mates. It is more appropriate, however, to consider the number of egg-laying *attempts* versus number of mates *encountered*, because encounters with a variety of potential hosts and prospective mates can provide individuals with valuable information. In many insects, the number of prospective mates encountered may be of an order of magnitude larger than the number of times an individual mates. This issue is discussed further below.

Because of the scarcity and potential bias of the few theoretical analyses of learning in the context of courtship and mating in insects, I examine the issue on the basis of general principles about animal learning.

Should insects learn in the context of sexual behaviour?

As mentioned in the introduction, insects learn in a wide variety of situations and such learning may have a great effect on fitness (Dukas and Bernays, 2000; Dukas, 2004a). I know of no theoretical reason to expect learning to have fewer benefits in the context of sexual behaviour compared to other behavioural categories. The major advantage of learning over innate behaviour is that it allows individuals to adjust to the specific conditions they experience at a certain place and time. Hence, if conditions such as mate signals and the relative quality of potential mates vary between locations and over time, learning may be beneficial (Stephens, 1991; Dukas, 1998).

In females, learning in the context of mate choice would enhance their ability to choose the relatively fitter male out of locally available alternatives. In many species, mate choice has been linked to direct and indirect benefits to females (Andersson, 1994; Moller and Alatalo, 1999; Moller and Jennions, 2001). For

example, females encountering many high quality males can learn to adopt a higher male acceptance criterion than females encountering only low quality males (Janetos, 1980; Reid and Stamps, 1997). The alternative to learning in the context of mate choice, which involves a fixed decision criterion, may result in choosing a relatively low quality mate where male quality is higher than the expected long-term average over many generations, or a postponement of mating and hence egg laying if the local male quality is lower than the expected long-term average. In males, learning in the context of courtship could help individuals focus their courtship efforts on those females most likely to accept them as mates. Furthermore, high quality males that can learn about their high mating success may rely on such learning to select and court high quality females. Hence, learning in the context of mate choice could provide fitness benefits to male and female insects. The key question then is whether typically there is variation in mate signals and quality which would make learning advantageous.

Variation in mate signals

In fruit flies (*Drosophila* spp), mate choice involves a dynamic exchange of information involving mostly acoustic and chemical signals (reviewed in Spieth, 1974; Spieth and Ringo, 1983; Greenspan and Ferveur, 2000). Both males and females of the most studied species, *Drosophila melanogaster*, exhibit large geographical variation in such signals. Jallon and David (1987) compared pheromonal composition of females from three *D. melanogaster* strains, Canton-S, Oregon and an Ivory Coast population. Proportions of the major female aphrodisiac, 7,11 heptacosadiene, were 0.28, 0.197 and 0.028, respectively, and proportions of the major anti-aphrodisiac, 7-tricosene, were 0.035, 0.05 and ~ 0 , respectively. Similarly, a worldwide comparison of females from 63 *D. melanogaster* strains revealed a range in the proportion of 7,11 heptacosadiene from 0.023 to 0.5 (Ferveur et al., 1996).

Male *Drosophila* produce species-specific courtship songs through wing vibrations. The major song component that varies between species is the period between two successive pulses, or the interpulse interval (IPI). Male *D. melanogaster* from eight distinct geographical locations showed significant between-locality variation in IPI, with the longest IPI being approximately 10% longer than the shortest IPI (Moulin et al., 2004). Indirect evidence also suggests rapid evolution of courtship song characteristics in the *D. Willistoni* species group (Ritchie and Gleason, 1995). Finally, in *D. melanogaster*, both the pheromonal composition and song components change with ontogeny in the males (Moulin et al., 2001, 2004) and the pheromonal composition changes with ontogeny and sexual receptivity in the females (Cook and Cook, 1975; Scott, 1986; Scott et al., 1988).

Variation in mate quality

In *D. melanogaster*, both males and females are sensitive to features that indicate mate quality. Virgin females are much more attractive to males than non-virgins,

and females that have mated in the distant past are more attractive than recently mated females (Cook and Cook, 1975; Scott, 1986; Scott et al., 1988). Similarly, the females prefer large over small males (Partridge and Farquhar, 1983; Partridge et al., 1987b; Dukas, 2005b) and select against males with depleted sperm resulting from recent matings (Markow et al., 1978).

In summary, at least in fruit flies, individuals exhibit variation in phenotypic traits that males rely on for choosing which females to court and traits that females use for choosing mates. Such variation could make learning in the context of sexual behaviour adaptive. Another necessary condition that would make learning advantageous over innate behaviour is that individuals must have the opportunity to gain relevant experience before making key sexual decisions. This issue is discussed in the following section.

Do insects have opportunities to learn in the context of sexual behaviour?

Female *D. melanogaster* have ample opportunities to learn in the context of mate choice. Most notably, female *D. melanogaster* typically reach sexual maturity only when they are 24-40 hours old (Manning, 1967). During that period, however, the immature, unreceptive females are vigorously courted by males (Manning, 1967; Dukas, 2005a). Furthermore, although recently mated female *D. melanogaster* typically become unreceptive and less attractive to males for several days, the females are still courted frequently (Manning, 1967; Cook and Cook, 1975; Dukas, 2005a). The experience gained during this second unreceptive period could be used if the females re-mate.

Male *D. melanogaster* also have many opportunities to learn whom to court. The males initiate courtship behaviour several hours after eclosion even though they are unlikely to be accepted as mates at this age (Long et al., 1980; Moulin et al., 2001, 2004). In male-male competition experiments involving trials with a single female and two males of different ages per test vial, 4-day-old males were almost twice as likely to mate as 2-day-old males, and 8-day-old males were about twice as likely to mate as 4-day-old males. In tests involving one female and one male per vial, all three male age classes had similar courtship latencies of about 1 min, and similar mating latencies of 4-7 min. The 2-day-old males, however, had lower fertility than the older age classes (Long et al., 1980). Young males also had lower levels of the sex pheromone, 7-tricosene, which peaked in 3-day-old males (Moulin et al., 2004). It is likely that the intense courtship activity by very young males serves primarily as an experience period which allows them to refine their courtship behaviour.

Therefore, even though fruit flies have an expected lifespan of several days and few mating opportunities, both males and females have many opportunities for gaining experience that could influence their mate choice and mating success. It is even possible that the emission of aphrodisiac pheromones in sexually immature females and courtship in sexually immature males may be adaptations for learning in the context of sexual behaviour.

Costs of learning

The net benefit from learning also depends on its costs. One can envisage three types of costs. First, learning may require extra neuronal machinery, which is costly to maintain. Second, maintaining information in memory probably requires continuous resource expenditure (Dukas, 1998, 1999; Laughlin et al., 1998; Laughlin, 2001; Mery and Kawecki, 2003, 2004, 2005). There is currently little empirical evidence regarding the physiological cost of learning. The best data available are for fruit flies (*D. melanogaster*). In one study, Mery and Kawecki (2003) found that artificial selection for learning ability in adult flies, which increased learning scores in the selected lines, was associated with reduced larval competitive ability under low food availability. In another study, Mery and Kawecki (2004) documented that adult flies from lines selected for improved learning ability had lower egg-laying rates than unselected lines when the flies of either line were exposed to alternating substrate conditions which required use of learning for substrate choice every 2 days under nutritional stress. Finally, Mery and Kawecki (2005) also documented that, compared to a few control treatments, flies that were subjected to a training regime that produced long-term memory showed earlier death in the absence of food and water. The latter two experiments suggest that associative learning has an operating cost paid for only by individual flies that learn (Mery and Kawecki, 2004).

Finally, some learning tasks require an individual to expend time and effort on gaining the necessary experience. For example, sexually mature females that postpone mating in order to gain experience of the locally available males could have lower fitness because of the associated delay in egg laying. However, as discussed in the section above, at least in *D. melanogaster*, females can gain substantial experience because they are courted by numerous males before reaching sexual maturity. Because both males and females can gain experience before sexual maturity, the sampling costs of learning in the context of sexual behaviour may be low. Sampling by immature individuals, however, may still be costly because it involves time, energy and exposure to danger. Indeed, in male fruit flies, courtship alone is associated with increased mortality rate even with no predation (Cordts and Partridge, 1996). In the females, male courtship may interfere with feeding and ovipositing (Wertheim et al., 2005). Furthermore, female avoidance behaviour, which could involve flying or running away, probably carries a small cost as well. These ecological costs of learning have not been quantified.

In summary, learning ability involves some maintenance and sampling costs. Although such costs may be hard to quantify, they must be considered because they reduce the net value of learning.

DATA

Neurogenetic work on courtship conditioning in fruit flies

The best evidence for learning in the context of courtship in insects involves fruit flies (*Drosophila melanogaster*). In the first study, Siegel and Hall (1979)

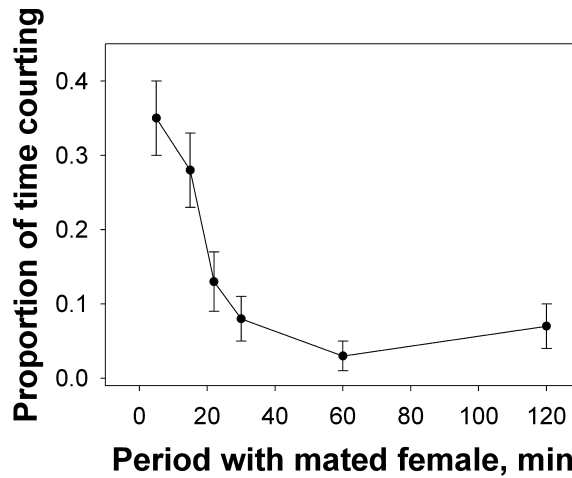


Figure 1. The effect of males' length of experience with recently mated female fruit flies on the subsequent proportion of time (mean \pm SE) spent courting anaesthetised virgin females. Data from Siegel and Hall (1979).

documented that males exposed to recently mated females significantly decreased their courtship effort within 30 min. To test for associative learning, males with experience of courting mated females for 5–120 min were subsequently presented with anaesthetised virgin females. By using anaesthetised females, the researchers controlled for variation in female behaviour which could influence the males. There was a strong negative correlation between the duration of male experience with mated females and their courtship duration with the anaesthetised virgin females (fig. 1). Siegel and Hall (1979) also compared wild-type males with *amnesiac* males that had a mutation that caused rapid memory decay. After 1 h of courting mated females, the flies experienced between 0–180 min time delay before being tested with anaesthetised virgin females. The *amnesiac* flies resumed regular courtship of the anaesthetised virgin females after a 30 min delay whereas the wild-type flies required 3 h for resuming regular courtship (fig. 2).

Further experiments using a variety of protocols and several learning and memory mutants established that associative learning underlies courtship conditioning (Tompkins et al., 1983; Gailey et al., 1984; Ackerman and Siegel, 1986; Zawisowski, 1988; McBride et al., 1999; Broughton et al., 2003; Ejima et al., 2005). Courtship conditioning is probably the simplest way of illustrating associative learning in individual fruit flies following the widely replicated protocol detailed in Connolly and Tully (1998, p. 312). It should be noted, however, that learning in fruit flies is not as robust as it is, for example, in honey bees. Hence variation in pheromones, behaviour and sexual receptivity among fly lines, and minute aspects of the protocol, such as the size and shape of test chambers, temperature, humidity and time of day, can influence the results.

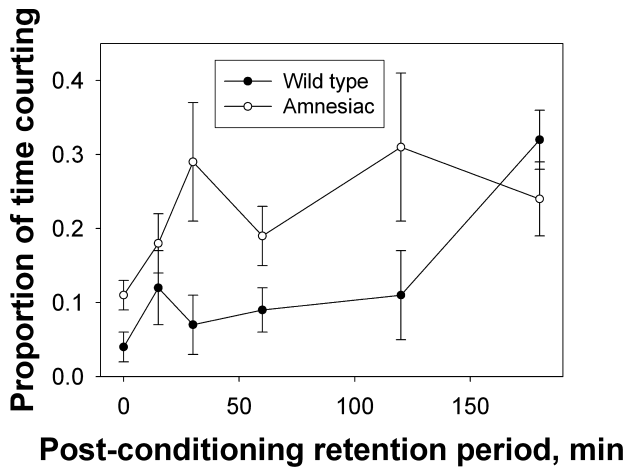


Figure 2. Effects of the post-conditioning retention interval on the subsequent average proportion of time (mean \pm SE) either wild-type (●) or *amnesiac* males (○) spent courting anesthetised virgin females. Data from Siegel and Hall (1979).

Evolutionary significance of learning in the context of courtship in fruit flies

The research just reviewed unambiguously established the role of learning in the context of sexual behaviour in fruit flies. I have recently tried to quantify the evolutionary significance of such learning. In an experiment with *D. melanogaster*, I allowed males to experience courting recently mated females for 1 h and then compared the levels of courtship by experienced males and those of inexperienced males towards either sexually receptive, virgin females or recently mated, unreceptive females. All females in the experiment were mobile and flies were always observed in standard 40 ml vials. Both the male treatments exhibited more intense courtship towards the sexually receptive, virgin females than the unreceptive mated females. However, the males with experience of mated females courted mated females half as often as the inexperienced males did (fig. 3). It should be noted that both male treatments courted the virgin females at similar intensities. This indicates that the reduced courtship towards mated females by the experienced males was not merely a result of male fatigue. Moreover, the experienced males were also faster to initiate courtship of virgin females and slower to start courting mated females, again indicating selective effects of learning (Dukas, 2005a).

In another experiment I assessed courtship intensity directed towards either virgin or mated females by males that had previously courted either recently mated females or immature virgin females for 1 h. Although both female types are sexually unreceptive, the sexually immature females are as attractive to males as sexually mature, virgin females (Manning, 1967; Tompkins et al., 1983). The experiment showed that males with experience of immature females were faster to court either virgin or mated females and showed higher courtship intensities towards virgin females compared with those males with experience of recently

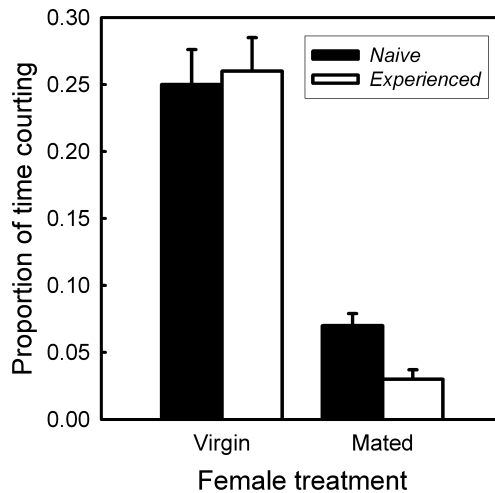


Figure 3. The proportion of time (mean \pm SE) that naïve males (■) and males experienced at courting mated females (□) spent courting either two virgin females or two mated females ($n = 320$ males) (Dukas, 2005a).

mated females. It seems that encountering soon-to-be sexually receptive, immature females heightened the courtship activity of the males (Dukas, 2005a). Even though the males with experience of immature females had not previously encountered mated females, the intensity of their courtship of mated females in the test was as low as that of the males with previous experience of mated females. The pheromonal profile of immature females is similar to that of sexually mature, virgin females and distinct from that of recently mated females, with the latter emitting higher levels of the anti-aphrodisiac pheromone, 7-tricosen (Scott, 1986; Scott et al., 1988). It is likely that males learned from their experience with the immature females about the expected levels of pheromones among sexually receptive females, and this caused them to show low levels of courtship on their first encounter with recently mated females (Dukas, 2005a).

The effects of learning discussed above suggest that male fruit flies narrow their acceptance threshold of females with experience in order to focus on courting females more likely to accept them as mates. This conclusion challenges the prevailing notion among evolutionary biologists that male fruit flies are rather indiscriminate (Wood and Ringo, 1980; Spieth and Ringo, 1983; Noor, 1996). Fruit flies have served as a central model system in research on incipient speciation (Coyne and Orr, 1989, 2004; Rice and Hostert, 1993). Evolutionary biologists, however, have, for the large part, ignored possible effects of learning on mate selection in fruit flies. I began to address the issue of learning in the context of incipient speciation by quantifying the effect of experience on interspecific courtship.

Previous research has indicated that male *D. melanogaster* readily court females of the closely related species, *D. simulans* (Manning, 1959; Wood and Ringo,

1980). The two species are visually similar but differ in their courtship songs and pheromonal profiles. The inter-pulse interval, a key parameter of the male courtship song, is about 50% shorter in *D. melanogaster* than in *D. simulans* (Schilcher and Manning, 1975; Kawanishi and Watanabe, 1980). Female *D. simulans* lack the cuticular hydrocarbon, 7,11-heptacosadiene, which is the major sex pheromone in female *D. melanogaster*. In contrast, female *D. simulans* possess higher levels of 7-tricosene than female *D. melanogaster* (Jallon and David, 1987). *D. melanogaster* and *D. simulans* have similar global geographic distributions. At a finer scale, *D. simulans* tends to occur farther from human habitations than *D. melanogaster* though the two species do occur sympatrically (Carracedo et al., 1985; Ashburner, 1989; Gromko and Markow, 1993; Markow, 2000). Hybridisations between the species have been recorded in nature and can be readily obtained in the laboratory with some strains (Sturtevant, 1920; Wood and Ringo, 1980; Izquierdo et al., 1992; Moulin et al., 2004).

In accordance with the previous research just mentioned, male *D. melanogaster* inexperienced with females exhibited similar courtship intensities towards female *D. melanogaster* and female *D. simulans*. However, male *D. melanogaster* with experience of courting female *D. simulans* showed a selective reduction in the proportion of time they courted female *D. simulans* (fig. 4). These results, which indicate that male fruit flies learn to narrow the range of females they are willing to court, suggest that levels of assortative mating, which could lead to incipient speciation, may be higher in fruit flies than commonly assumed by evolutionary biologists (Dukas, 2004b).

Inexperienced, sexually mature male fruit flies (*D. melanogaster*) also court immature males, although mature males quickly habituate to the young males and

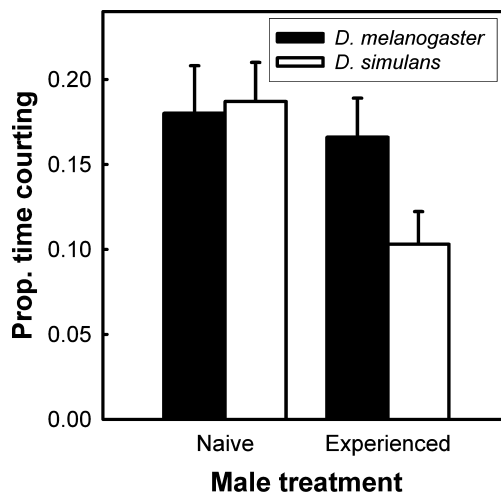


Figure 4. The proportion of time (mean \pm SE) either naïve males or males experienced at courting female *D. simulans* spent courting either two female *D. melanogaster* (■) or two female *D. simulans* (□) ($n = 192$ males) (Dukas, 2004b).

stop courting them (Gailey et al., 1982). In a laboratory study with the *Dunce* mutant, which diminishes learning, Gailey et al. (1985) documented a significant mating advantage of wild-type flies over *Dunce* flies when placed together with one virgin female and nine immature males. Whereas the wild-type flies learned to avoid courting the immature males and selectively courted the single virgin female, the learning mutants spent much of their time courting the immature males. In a control experiment, Gailey et al. (1985) found no difference in the mating frequencies of wild-type flies and *Dunce* flies either when males of the two fly types were placed together with only a single virgin female, or when each male was placed singly with a single female. This set of experiments indicates the potential benefit from learning in the context of courtship by males.

Learning by female fruit flies in the context of mate choice

As discussed in the theory section, female insects could also benefit from learning in the context of sexual behaviour. That issue has been critically addressed recently. Large *D. melanogaster* males have higher mating success than small males (Partridge and Farquhar, 1983; Partridge et al., 1987a, b). Because male size can vary greatly in space and time, experience with the local males would enable females to adjust the size threshold for accepting potential mates. To test for such an effect of learning on mate choice, I allowed young virgin females to experience courtship, but no mating, with either small or large flies for 2 h. On the following day, half the females from each treatment were placed with small males and half were placed with large males. Compared with the females that experienced courtship by large males, females that experienced courtship by small males were significantly more likely to mate with small males (Dukas, 2005b). These results suggest that female fruit flies learn to adjust their mate acceptance criterion.

Learning in the context of sexual behaviour in other insects

A variety of studies on insects suggested that learning influenced sexual behaviour. Here I review briefly some of the suggestive evidence from insects other than fruit flies. Much of this work requires further research to verify and quantify with proper controls the effects of learning on courtship and mating.

Males

First, there is replicable evidence from a few species of solitary bees that females have individually distinctive odours. Males who unsuccessfully court one female habituate to her but show higher courtship intensity when exposed to another female (Barrows et al., 1975; Greenberg, 1982; Smith, 1983; Wcislo, 1987, 1992). Second, a number of studies suggest that in species in which males provide females with food gifts, males rely on experience to optimally adjust gift size. A male providing a larger gift may father more offspring with the current female, but the male's limited

resources may reduce his subsequent mating success. Hence the male may choose to reduce gift size if one mating is likely to be followed by another (Bussiere et al., 2005). For example, Bussiere et al. (2005) manipulated the encounter rates with conspecifics in male tree crickets (*Oecanthus nigricornis*). Males of the female-biased treatment encountered, but could not mate with, a series of 12 distinct females over a period of 3 days. Males of the male-biased treatment encountered a series of 12 distinct males during the same period. Afterwards, all the males were allowed to mate with a single female. Indirect measures suggested that males from the male-biased treatment provided the females with larger gifts than did those from the female-biased treatment.

Females

First, the pine engraver (*Ips pini*) is a small, polygynous bark beetle in which males provide resources to their mates and offspring. Each male engraves a mating chamber under a tree bark. Prospecting females typically inspect a few chambers before accepting a male, which may be their sole life-time mate. In a field study, females in patches with high male quality exhibited higher male acceptance thresholds than females in patches with low male quality (Reid and Stamps, 1997). Second, female crickets (*Gryllus lineaticeps*) typically prefer male calling songs with high chirp rates over calling songs with low chirp rates. In a laboratory experiment, females showed lower responses to male calls with low chirp rates after listening to calls with high chirp rates than after listening to calls with low chirp rates (Wagner et al., 2001). Third, female crickets (*G. bimaculatus*) prefer large over small males. Females that were mated with either small or large males were later tested for their willingness to mate with a second male that was either small or large. Whereas females that had mated with small males accepted large males as second mates in over 90% of the trials, females that had mated with large males accepted small males as second mates in less than 50% of the trials (Bateman et al., 2001).

Negative data

Some studies have documented no effects of experience on sexual behaviour in insects. For example, female seaweed flies (*Coelopa frigida*) are promiscuous and remain sexually receptive after mating. Larger males have higher mating successes than small males. However, controlled experiments failed to document that the size of the first mate affected a female's subsequent preference for mate size (Shuker and Day, 2002). It is typically difficult to interpret results that suggest no learning because one could argue that an alternative protocol would document significant effects of learning. It is possible that there is between-species variation in the use of learning for courtship and mate choice and this issue requires further evaluation.

PROSPECTS

The above review indicates that the conditions necessary for the evolution and maintenance of learning in the context of sexual behaviour exist in at least a few insect species that exhibit such learning. Currently, we have only a limited understanding of learning in the context of sexual behaviour. Insects could serve as a key group for enhancing this gap in our knowledge. Some of the central issues requiring future research are: i) the prevalence of variation in signals and quality among potential mates; ii) the learning opportunities males and females have before mating; iii) the potential net benefit from such learning; iv) the overall prevalence of learning in the context of sexual behaviour in insects; v) the type of information male and female insects learn about courtship and mating; and vi) the effects of learning on sexual selection and incipient speciation.

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