



Courtship strategies of male insects: when is learning advantageous?

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Experiments indicating learning in the context of courtship in fruit flies challenge the prevailing views that male insects are either indiscriminate or rely on innate rules for courtship. We investigated the conditions favouring learning during courtship in insects by using a model that compared a learning strategy to two alternatives, indiscriminate courtship and innate selectivity. Our analyses indicated that, under the two conditions of high encounter rates with females and long courtship durations, indiscriminate courtship resulted in much lower lifetime mating success than either selectivity or learning. Learning had moderate advantages over selectivity when encounter rates with females were high, when a large proportion of females were sexually receptive, and when acceptance rates by sexually receptive females were high. We predict that species in which such conditions commonly occur are most likely to show learning in the context of male courtship.

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In the vast majority of animals, females invest more resources in reproduction than males. This, and the consequent high ratio of sexually active males to fertilizable females, causes males to court females somewhat indiscriminately, whereas females are selective while choosing mates (Bateman 1948; Emlen & Oring 1977; Andersson 1994). Indiscriminate courtship is often rather extreme in males of many insects, which seem to consider various objects approximating conspecific females in size or odour as courtship targets. For example, several experiments with fruit flies (*Drosophila* spp.) have documented that courting males show either complete or partial failure to distinguish between intraspecific and interspecific females (Wood & Ringo 1980; Spieth & Ringo 1983; Noor 1996). The relative indiscriminate courtship in male insects has been attributed to their short life span and lack of opportunities to learn about potential mates. This is in contrast to most birds and mammals, in which young typically interact with their caring parents and hence

can learn about the traits characterizing sexually mature conspecifics (Alexander et al. 1997; Dukas 2006).

The prevailing assertion about indiscriminate courtship by male insects has been challenged by analyses of the role of learning in the context of courtship by male fruit flies, *D. melanogaster*. First, even though inexperienced *D. melanogaster* males court conspecific females and females of the closely related *D. simulans* at similar intensities, the males can learn to reduce courting of female *D. simulans*, which typically reject all mating attempts by male *D. melanogaster* (Dukas 2004). Second, male *D. melanogaster* experienced at courting recently mated unreceptive females learn to selectively avoid recently mated females but not receptive virgin females (Dukas 2005).

The data on learning in the context of courtship by male fruit flies suggest that indiscriminate male courtship may not always be optimal. It is not clear, however, when learning in the context of courtship would be the optimal male strategy. Would we expect such learning to be common among insects? Are mature, experienced male insects much more selective than has been commonly assumed? Answers to such questions can help us better understand courtship behaviour and its effects on processes of sexual selection and incipient speciation, which may be affected by learning. For example, learning could increase levels of assortative mating (Irwin & Price

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1999; ten Cate & Vos 1999; Lachlan & Servedio 2004; Belman & Metz 2005).

To evaluate learning in the context of courtship, we constructed a stochastic optimization model of male courtship behaviour. Our model is similar to a signal detection model (Green 1966; Wiley 1994; Getty 1996) in which the decision criterion is adjusted using Bayesian updating (Clark & Mangel 2000). Unlike most mate choice models, which focus on the female choosing a single mate (Janetos 1980; Wiegmann et al. 1996), our model considers the question of whether a male encountering a female should court her or keep searching for other females. The male is willing to mate with any sexually receptive conspecific female who accepts him and he may court and mate with many females over time. We addressed two key questions. First, what realistic courtship strategies might male insects possess? Second, under what conditions would learning in the context of courtship contribute to higher fitness than the nonlearning alternatives? We parameterized our model using data from *D. melanogaster*. Conceptually, however, our model is relevant for a variety of insects, as well as other taxa in which parents do not interact with their offspring.

MALES' COURTSHIP STRATEGIES

Ideally, male insects would court only sexually receptive, conspecific females. For two reasons, however, males cannot always distinguish between sexually receptive, conspecific females and unreceptive females. First, to identify receptive females, male insects rely primarily on sex pheromones. The composition of these pheromones varies among individuals and populations, during a female ontogeny and with female mating history, and over generations (Cook & Cook 1975; Jallon & David 1987; Scott et al. 1988; Ferveur et al. 1996). Second, as a result of the large pheromonal variation within and between species in time and space, the pheromonal distribution of sexually receptive conspecific females may partially overlap with that of unreceptive conspecific and interspecific females.

Given that identifying sexually receptive females may be a formidable task, the traditional scenario, in which indiscriminate males simply approach anything resembling a conspecific receptive female, does seem reasonable. On the one hand, the cost of initiating numerous courtships may be rather low, although it is known to be non-zero (Cordts & Partridge 1996). On the other hand, if sexually receptive females are relatively rare, it may be advantageous for males to avoid any selective courtship strategies that might reduce males' probability of mating with a rare sexually receptive female.

Between the two extremes of courtship behaviour based on perfect knowledge, which is unrealistic, and feasible indiscriminate courtship lie two other possible courtship strategies. First, males may rely on an innate template to decide whether to court a female or not. For example, males may only court females producing sex-specific pheromones above some threshold level. We term this strategy selective courtship. Second, inexperienced males

may have some initial innate template, which they update with experience. This is the learning strategy.

To compare the three feasible alternatives just discussed (indiscrimination, innate selectivity and learning), we first develop a basic model, which assumes that males have a perfect knowledge about female pheromonal distributions that remain constant over space and time. We then relax this assumption to deal with the realistic case of males encountering female pheromonal distributions that vary over space and time.

Our model does not explicitly address temporal variation and costs of learning because these topics have already been well evaluated (e.g. Stephens 1991, 1993; Dukas 1998). Rather, we focus on the development and comparison of the three feasible courtship strategies outlined above, allowing for variation in female pheromonal distribution, but ignoring the costs of learning. The latter issue is addressed in the discussion.

The Basic Model

We assume that the males search for sexually receptive females at a food patch containing numerous flies varying in their pheromonal signal, x . Sexually receptive females are conspecific females that are either virgin or previously mated females that are ready to remate. Such females may either reject a courting male or accept him as a mate. The flies are divided into two categories:

V = sexually receptive females

N = any other fly

Let $f_V(x)$ be the probability density for x , for V flies, such that

$$f_V(x)dx = \Pr(V \text{ has pheromone signal in } (x, x + dx))$$

Similarly $f_N(x)$ refers to N flies. These are assumed to be normal distributions with mean μ_V and μ_N , and variances σ_V^2 , σ_N^2 . Different populations of flies have different distributions.

For simplicity, assume that $f_N(x)$ is always the same, but that μ_V varies between populations (but σ_V^2 is constant).

Additional parameters:

ρ = rate of encountering flies (V or N) (flies/min)

λ = proportion of flies that are V

p_s = probability that a V fly accepts a courting male

t_c = courtship duration

t_m = mating duration

Assume that the male's courting strategy is: court if and only if

$$a \leq x \leq b,$$

where a and b are constants to be determined later. We assume that the male can determine x for each fly encountered. If the x interval is large, the male will court often. He will be less likely to bypass V females, but many of the flies courted will be unreceptive females, N s. If the interval is small, the male is more selective, but he may miss out on some sexually receptive females, V s.

For simplicity, assume also that

$$\mu_N < \mu_V$$

(Fig. 1). This assumption is realistic because it implies that sexually receptive females appear more attractive than unreceptive females. Then, clearly, the optimal courting strategy has $b = +\infty$, so the strategies to be considered are of the form:

court if and only if $x \geq a$.

Again, large a means few flies are courted, but most are V s, and vice versa.

Also, large a means that many V s are not courted.

The Simple Case: Female Pheromones Are Fixed

We first assume that the pheromonal distributions of sexually receptive females and other flies are fixed over time and space. Given this assumption, we can also assume that the males have perfect knowledge about the pheromonal distributions, so they can have a fixed innate preference for the pheromonal signals indicating sexually receptive females. With these assumptions, we can calculate the males' optimal courting strategy.

Let T be a long search time. Then, using averages, we have number of encounters $= \rho T$

number of V s encountered $= \lambda \rho T$. Also,

$$\begin{aligned} & \text{Pr}(\text{court given an encounter}) \\ &= \text{Pr}(V) \times \text{Pr}(\text{court}|V) + \text{Pr}(N) \times \text{Pr}(\text{court}|N) \\ &= \lambda \text{Pr}(x \in [a, b]|V) + (1 - \lambda) \text{Pr}(x \in [a, b]|N) \\ &= \lambda \int_a^b f_V(x) dx + (1 - \lambda) \int_a^b f_N(x) dx. \end{aligned}$$

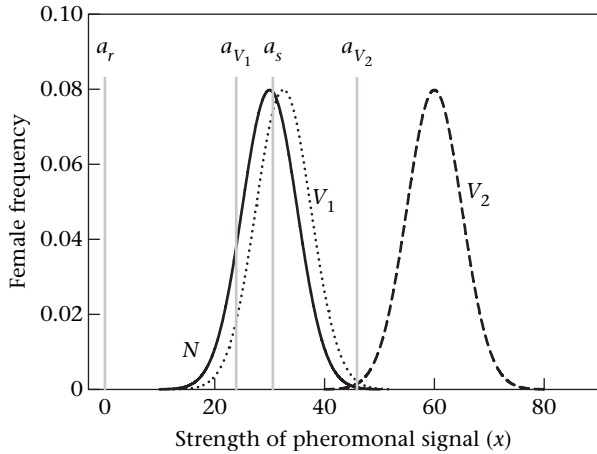


Figure 1. The assumed frequency distribution of pheromones of sexually unreceptive flies (N) and sexually receptive females of population V_1 and population V_2 as used in model calculations and simulations. The average pheromonal profiles are $\mu_N = 30$, $\mu_{V_1} = 32.5$ and $\mu_{V_2} = 60$, all with $SD = 5$. The four vertical lines indicate the values of a , which is the pheromonal strength, x , above which a male using a given strategy should court. Indiscriminate males court all females ($a_r = 0$). Selective males use the optimal value a_s . Learning males commence with a_s and then, based on their experience within a given female population, update their decision criterion towards either a_{V_1} or a_{V_2} , which are the optimal values for female populations V_1 and V_2 , respectively, for males with perfect knowledge. The optimal values of a are for the base parameters, $\rho = 1$ per min, $\lambda = 0.01$, $p_s = 0.2$, $t_c = 1$ min and $t_m = 20$ min.

Therefore,

$$\text{number of courtings} = \rho T \int_a^b [\lambda f_V(x) + (1 - \lambda) f_N(x)] dx$$

and

$$\text{number of successful courtings} = \rho T \lambda \int_a^b f_V(x) dx \times p_s.$$

Combining these, we get

$$\begin{aligned} & \text{rate of successful courting} \\ &= \frac{\text{number of successes}}{\text{total time (searching and courting)}} \end{aligned}$$

or

$$R = \frac{\lambda \rho p_s \int_a^b f_V(x) dx}{1 + \rho t_c \int_a^b [\lambda f_V(x) + (1 - \lambda) f_N(x)] dx} \quad (1)$$

(because the factor T cancels out from each term).

Equation (1) ignores the extra time spent mating after a female's acceptance. To incorporate this time, t_m , we add the term

$$\rho t_m \int_a^b \lambda f_V(x) dx \times p_s$$

to the denominator. This gives

$$R = \frac{\lambda \rho p_s \int_a^b f_V(x) dx}{1 + \rho \int_a^b [\lambda (t_c + p_s t_m) f_V(x) + (1 - \lambda) t_c f_N(x)] dx} \quad (2)$$

The optimal courting strategy maximizes R . Because we assume that $b = +\infty$, this is just maximizing with respect to a . That is, we can use equation (2) to determine the optimal pheromonal threshold, a , above which the males should court females to maximize their rate of mating.

The optimal courting strategy based on equation (2) assumes that the males have perfect knowledge about the presumably fixed pheromonal distributions of sexually receptive females and other flies. As discussed above, this assumption is not met in a variety of insects. Hence we proceed to investigate realistic settings involving female pheromonal distributions that vary in space and time.

The Realistic Case: Female Pheromones Vary in Space and Time

We now assume that μ_V , the mean pheromone signal for sexually receptive females, varies between populations and generations. We consider three ways that males can cope with this variation. First, the males can simply be

indiscriminate and court all females encountered. Second, the males may use an innate optimal courtship threshold that maximizes the expected long-term rate of mating. We term this the selective strategy. Finally, the males may commence with an innate courtship threshold that they keep updating based on experience. We model this learning strategy using Bayes' theorem (see [Appendix](#)).

Comparing the courtship strategies

We compared the mating success of the three feasible courting strategies, indiscriminate, selective and learning. The males adopting each of the three strategies had equal probabilities of being either in (1) a population consisting of sexually unreceptive flies, N (with $\mu_N = 30$), and sexually receptive females of population V_1 (with $\mu_{V_1} = 32.5$), or in (2) a population consisting of sexually unreceptive flies, N (with $\mu_N = 30$), and sexually receptive females of population V_2 (with $\mu_{V_2} = 60$; [Fig. 1](#)). First, for the indiscriminate males, we calculated the expected rate of mating, R (equation (2)), assuming that the indiscriminate males court all females encountered. Second, for the selective males, we assumed a fixed courtship decision criterion that maximized the expected rate of mating, R , given that the selective males had an equal probability of being in populations containing either V_1 or V_2 females. This was done by maximizing

$$\frac{1}{2}R[a, \mu_V = \mu_{V_1} = 32.5] + \frac{1}{2}R[a, \mu_V = \mu_{V_2} = 60]$$

with respect to a , where $R[a, \mu_V = \mu_{V_1} = 32.5]$ is equation (2) with μ_V set to 32.5 and $R[a, \mu_V = \mu_{V_2} = 60]$ is equation (2) with μ_V set to 60 ([Fig. 1](#)).

Finally, for the learning strategy, we ran simulations using the strategy outlined in the [Appendix](#). Briefly, the male searches for females. If he encounters a female, he measures her pheromonal signal, x , and updates his innate estimate, which, initially, is the selective strategy just described. The male uses the current Bayesian estimate and equation (2) to decide whether to court. If the male courts, he updates the Bayesian estimate based on the female's response. The male then repeats the above steps until death. For all three strategies, we assumed a total of 600 min devoted to courtship activity, including searching for mates, courtship and mating, and used the base parameters, $\rho = 1$ fly per min, $\lambda = 0.01$, $p_S = 0.2$, $t_c = 1$ min and $t_m = 20$ min ([Spieth 1974](#); [O'Dell 2003](#); [Dukas 2005](#)).

RESULTS

With the base parameters ([Fig. 2](#), middle group of bars), the mating success of learning males was approximately 7% higher than that of selective males and 22% higher than that of indiscriminate males. The advantage of learning over selectivity remained about the same when the encounter rates with females were higher ([Fig. 2](#), two right groups of bars), but the mating success of learning and selective males were virtually identical under lower encounter rates with females ([Fig. 2](#), two left groups of bars). The indiscriminate strategy yielded mating success similar to

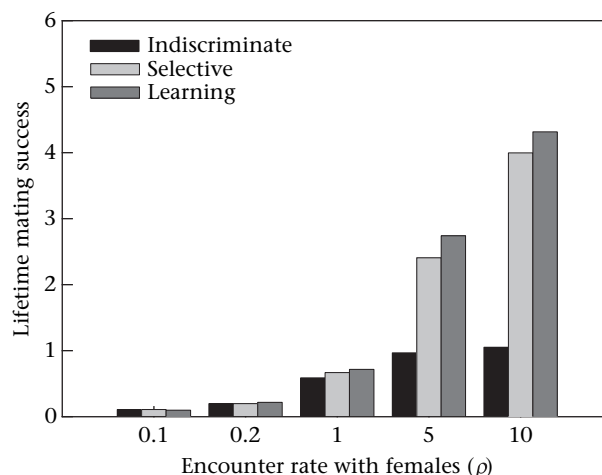


Figure 2. The lifetime number of matings of males using the indiscriminate, selective and learning strategies. The results are based on 600 min of lifetime courtship for the base parameters (the middle group of bars, $\rho = 0.1$) and two lower and two higher values of ρ , the encounter rate with females (see legend for [Fig. 1](#) for other parameter values).

selectivity and learning under low female encounter rates but performed relatively poorly with high female encounter rates. [Figures 3 and 4](#) help to explain these results. The curves in [Fig. 3](#) depict relative mating rates for males adopting a decision criterion, a , varying from 0 to 90 such that the males court any female with pheromonal signal, $x \geq a$. Our numerical calculations assume that the males encounter sexually unreceptive females and one of two sexually receptive female populations as illustrated in [Fig. 1](#). Hence the curves in [Fig. 3](#) show relative mating rates for each of the two sexually receptive female populations, V_1 and V_2 . With the base parameters ([Fig. 3a](#)), the optimal value of $a = 32$ for the selective males yielded relative mating rates of s_{V_1} and s_{V_2} when in population V_1 and V_2 , respectively. The average of these rates, which is the expected mating rate of selective males, was higher than that of the indiscriminate males (r), who court all females (i.e. they use $a = 0$).

The learning males start with the a value used by selective males, which assumes an equal a priori probability of being in a population with either V_1 or V_2 females. The learning males, however, keep updating their estimate of the average pheromonal signal of sexually receptive females. This updating is depicted as learning curves in [Fig. 4](#). With the base parameters ([Fig. 4a](#)), learning males in a population with V_1 females gradually improved their estimate of their probability of encountering V_1 females. This resulted in a gradual increase in mating rates from s_{V_1} towards a_{V_1} ([Fig. 3a](#)). Intriguingly, learning males in a population with V_2 females initially reduce their estimate of their probability of encountering V_2 females ([Fig. 4a](#)). The reason for this nonintuitive outcome is that, with the realistic base parameter of 1% encounter rates with sexually receptive females, experience with unreceptive females can initially mislead the males to decrease their estimate of the average pheromonal signal of sexually receptive females. The initial dip in the learning

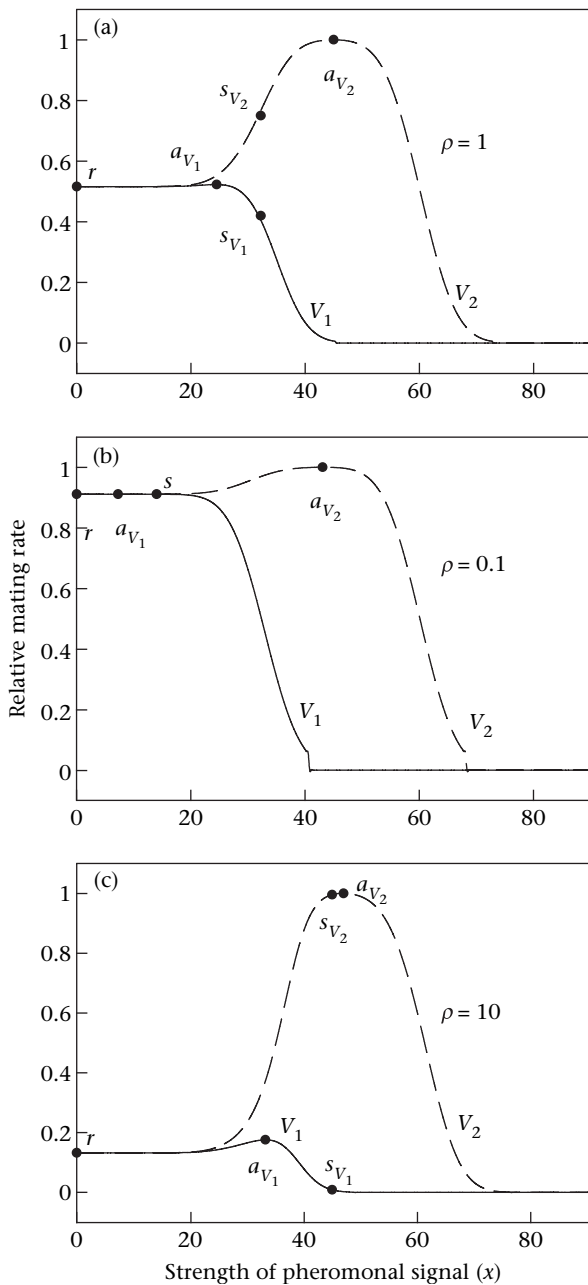


Figure 3. The relative mating rates of males encountering sexually unreceptive flies (N) and sexually receptive females of either population V_1 (solid curves) or population V_2 (dotted curves) as a function of a , which is the pheromonal strength, x , above which a male courts. The mating rates are standardized such that $a_{V_2} = 1$ in each panel to allow for easy comparisons among the mating strategies. Indicated on each curve are the mating rates of indiscriminate males (r), selective males (s) and males with perfect knowledge (a). Where relevant, the sexually receptive female population (either V_1 or V_2) is noted in the subscripts. The learning males, which initially adopt the selective strategy (s), update their decision criterion towards either a_{V_1} or a_{V_2} (in populations V_1 or V_2 , respectively) and gain a corresponding increase in mating rates with experience. The three panels are for (a) the base parameters, (b) encounter rate with females, $\rho = 0.1$ and (c) $\rho = 10$.

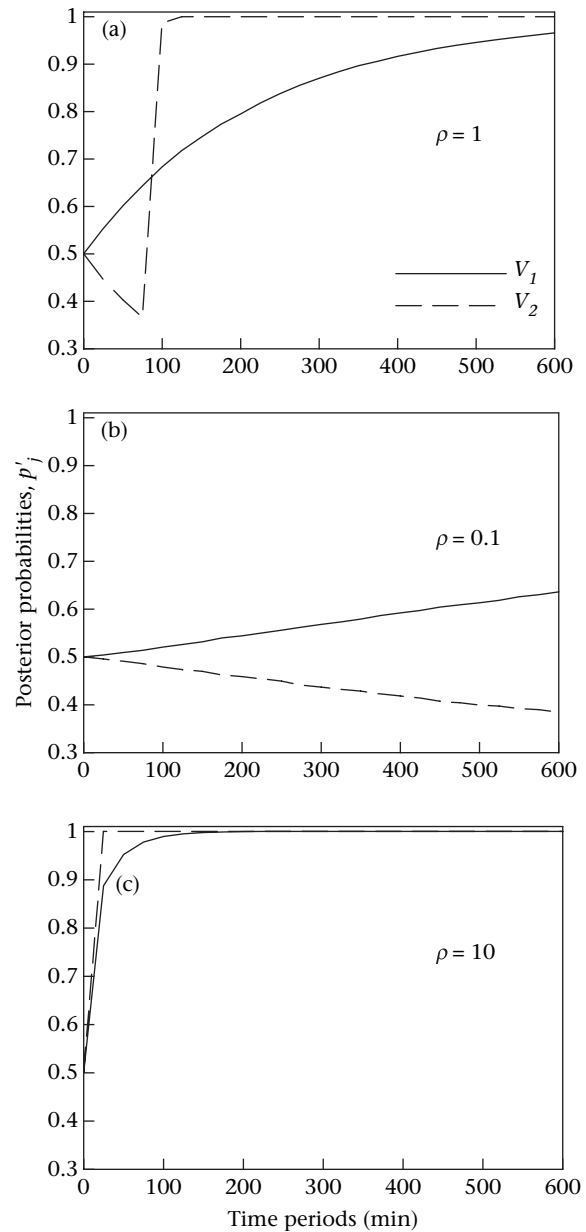


Figure 4. The change over time in learning males' correct estimate of the probability that they encounter females from either population V_1 (solid curve) or population V_2 (dotted curve). A value of 1 means that the males are correctly certain of which population they are actually in. A value of 0.5 means that the males consider it equally likely that they are in either population. A value of 0 means that the males are incorrectly certain of which population they are actually in. In our numerical examples, the males begin with the a priori probability, $p_j = 0.5$. They then update their estimate, generating the posterior probabilities, p'_j , based on their encounters with females, and p''_j , based on females' responses to the males' courtship if the males choose to court (see Appendix). Each posterior probability becomes the a priori probability for the next encounter with female and so on for successive encounters. The three panels depict posterior probabilities for the (a) base parameters (see legend for Fig. 1), (b) the encounter rate with females, $\rho = 0.1$ and (c) $\rho = 10$.

curve was followed by a sharp increase when the males first encountered a V_2 female (Fig. 4a). This increase was associated with a large increase in mating rate from S_{V_2} towards a_{V_2} (Fig. 3a).

Figures 3 and 4 also illustrate why the results changed dramatically when the encounter rate with females was decreased to 10% that of the base parameter (to $\rho = 0.1$; Fig. 2). The low female encounter rate constrained mating, resulting in similar mating rates for the indiscriminate and selective males (Fig. 3b). The expected average mating rate with perfect knowledge (the average of a_{V_1} and a_{V_2}) was higher, but, as illustrated in Fig. 4b, the low female encounter rate (i.e. small number of learning trials) was also a constraint on learning. This means that, on average, the learning males gain no benefit from learning under this set of parameters.

Increasing the encounter rate with females by a factor of 10 (to $\rho = 10$) magnifies the relative advantage of selectivity and learning over indiscrimination (Fig. 2). In this case, the optimal value of a for selective males accommodates the large advantage from overestimating the probability of encountering V_2 (rather than V_1) females. Hence, on average, the selective males performed four times better than indiscriminate males even though, with V_1 females, their mating rates were lower than those of indiscriminate males (Fig. 3c). The learning males can learn quickly about the pheromonal distribution of sexually receptive females (Fig. 4c). This, however, does not translate into a large increase in mating rates compared to selectivity. On the one hand, with V_2 females, selectivity alone performed well, so there was little opportunity to improve from s_{V_2} towards a_{V_2} (Fig. 3c). On the other hand, the shape of the mating-rate curve with V_1 females was rather shallow, hence moving from s_{V_1} towards a_{V_1} provided only little mating advantage.

Figures 5–7 illustrate the effect of modifying three other model parameters. Note that we chose to change the base parameters (the middle group of bars in each graph) by factors of 5 and 10 except for probability of mating with sexually receptive females (Fig. 6), which can have a maximum value of 1. Overall, mating success showed obvious positive correlations with the proportion of sexually receptive females (Fig. 5) and the probability of mating with sexually receptive females (Fig. 6) and a negative correlation with courtship duration (Fig. 7). However, the absolute and relative magnitudes of the effect of varying these three parameter values on mating success with the three courtship strategies were different.

Increasing the proportion of virgin females had a strong effect on mating success, but the effect was similar with all three strategies (Fig. 5). The reason is that changing the proportion of sexually receptive females caused a corresponding change in absolute mating rates but the relative mating rates, depicted for the base parameters in Fig. 3a, remained virtually identical (for conciseness, we do not present graphs for other λ values because they were similar to Fig. 3a). The learning rates for the lowest and highest λ values were similar to those for the lowest and highest ρ values, respectively (Fig. 4b, c). Here, however, learning males maintained their small advantage over selective and indiscriminate males even for the lowest λ value. In

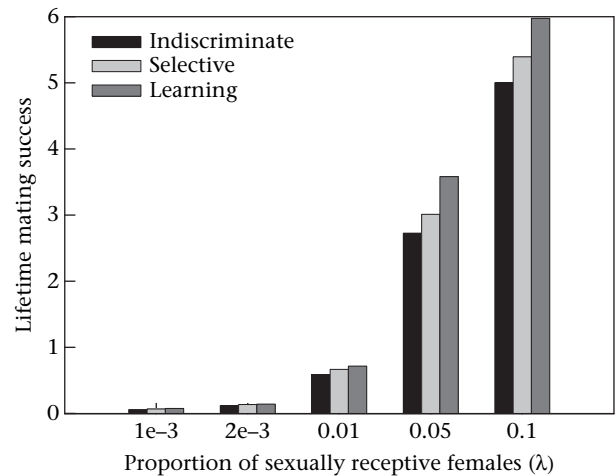


Figure 5. Lifetime mating success of males using the indiscriminate, selective and learning strategies. The results are based on 600 min of lifetime courtship for the base parameters (the middle group of bars, $\lambda = 0.01$) and two lower and two higher values of λ , the proportion of females that are sexually receptive (see legend for Fig. 1 for other parameter values).

this case, learning males in V_2 female populations who encounter (with the low probability of 0.001) a sexually receptive female can sharply shift their decision criterion towards a_{V_2} and gain substantially higher mating rates. However, learning males who do not encounter a sexually receptive female only change their decision criterion very little towards a_{V_1} . This causes a relatively little loss in expected mating rates only when the learning males are in a V_2 female population (see Figs 3a, 4b). That is, different types of experience have distinct effects on learning and mating success.

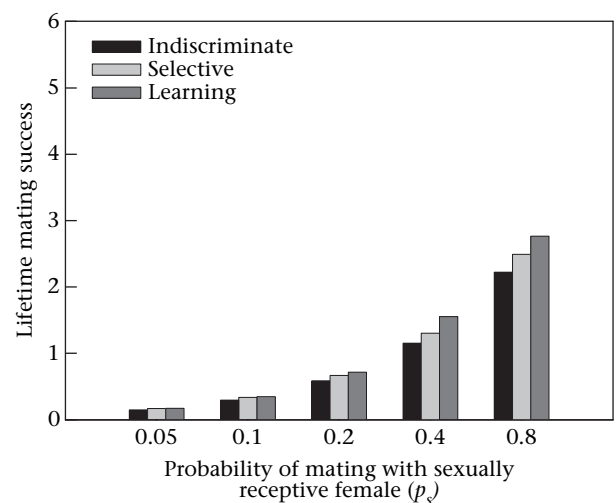


Figure 6. Lifetime mating success of males using the indiscriminate, selective and learning strategies. The results are based on 600 min of lifetime courtship for the base parameters (the middle group of bars, $p_s = 0.2$) and two lower and two higher values of p_s , the probability that a sexually receptive female mates with a courting male (see legend for Fig. 1 for other parameter values).

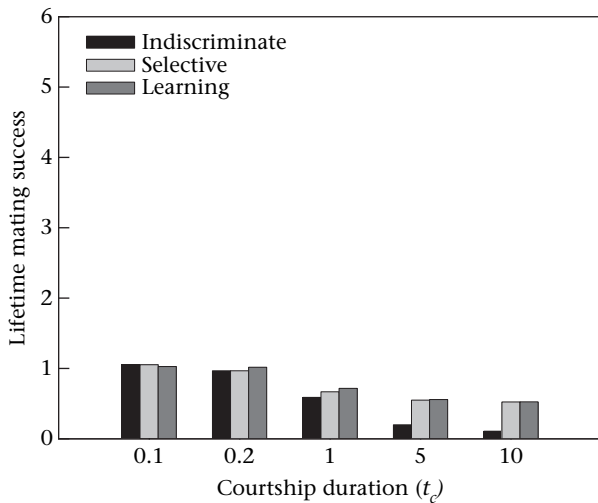


Figure 7. Lifetime mating success of males using the indiscriminate, selective and learning strategies. The results are based on 600 min of lifetime courtship for the base parameters (the middle group of bars, $t_c = 1$) and two lower and two higher values of t_c , the duration of each courtship event (see legend for Fig. 1 for other parameter values).

Varying the probability of mating with sexually receptive females (Fig. 6) had similar effects on mating success as varying the proportion of sexually receptive females (Fig. 5; note the different relative scales on the X axes of Figs 5, 6). The informational effects, however, are somewhat different (Fig. 8). With the base parameters ($p_s = 0.2$), males with V_1 females learned very slowly about the average pheromonal distribution of the sexually receptive females (Fig. 4a). This is because the pheromonal distribution of V_1 females is similar to that of unreceptive females (Fig. 1) and V_1 females reject courting males in 80% of courting events. In contrast, when V_1 females

accept courting males in 80% of courting events ($p_s = 0.8$), the males can learn faster that they encounter V_1 females (Fig. 8).

Finally, compared to the other three parameters just discussed (Figs 2, 5, 6), varying courtship duration had the least effect on mating success. This is because mating rates are limited by other factors such as the rate of encountering females, the proportion of sexually receptive females, the probability of acceptance by sexually receptive females and mating duration. When courtship duration is very short (left groups of bars in Fig. 7), indiscrimination is as successful as selectivity and learning because the time cost of courting sexually unreceptive females is relatively small. Long courtship durations (right groups of bars in Fig. 7) imply large time costs for indiscrimination and low mating success relative to the alternatives. Under both low and high values of courtship duration, learning and selectivity result in similar mating success. With low courtship duration, there is little to gain from learning because even the extreme strategy of indiscrimination is relatively successful. That is, the shape of relative mating success as a function of a was shallow (as in Fig. 3b), so even using the optimal a values assuming perfect information (a_{V_1} and a_{V_2} ; Fig. 3b) provided little advantage. For high values of courtship duration, the optimal decision criterion for selective males was close to that for the optimal decision criterion under perfect information in population V_2 . Hence learners gain little relative to selective males in population V_2 . The learners also gain little relative to selective males in population V_1 because of the shallow curve of relative mating rate as a function of a for that population (similar to Fig. 3c).

DISCUSSION

Learning versus Null Models

Under most of the conditions examined, learning in the context of courtship conferred small advantages over innate selectivity, which was usually somewhat better than indiscriminate courtship. Learning and selectivity resulted in much higher lifetime mating success than indiscriminate courtship under the two conditions of relatively high encounter rates with females (Fig. 2) and relatively long courtship durations (Fig. 7). Of these two conditions, learning was advantageous over selectivity only under high encounter rates with females. Based on these results, we predict that learning in the context of male courtship is most likely to be documented in species in which males experience high encounter rates with females. Two additional conditions where learning in the context of male courtship is more likely to occur given its relative advantage over the nonlearning alternatives are large proportions of sexually receptive females (Fig. 5) and high acceptance rates by sexually receptive females (Fig. 6). These two cases appear to be prevalent in insects, as indicated by numerous cases of female polyandry and mate choice by males (Arnqvist & Nilsson 2000; Bonduriansky 2001; Simmons 2005).

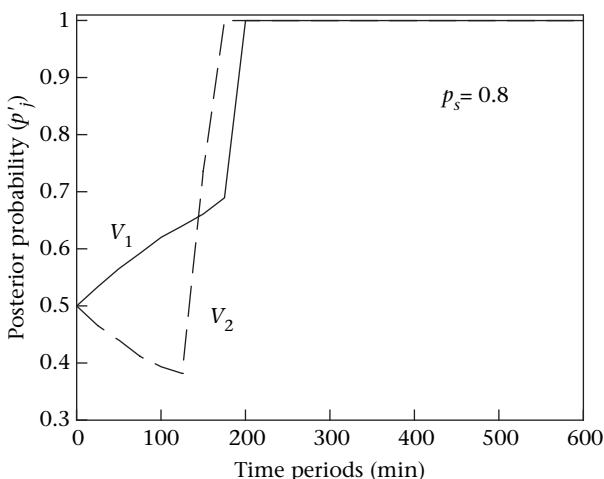


Figure 8. The change over time in the learning males' correct estimate of the probability that they encounter females from either population V_1 (solid curve) or population V_2 (dotted curve). The curves are for all base parameters (see legend for Fig. 1) except for $p_s = 0.8$. See legend for Fig. 4 for further details, and Fig. 4a for the corresponding curves with $p_s = 0.2$.

We should note that, on the one hand, even small fitness benefits may help to maintain learning in the context of male courtship, so such learning may occur even in settings that we did not highlight above. On the other hand, if learning indeed provides relatively small advantages under many settings, it may be hard to empirically quantify the value of learning in the context of courtship. Furthermore, our model illustrates how even systematic observations of courting males who use either selective or learning strategies might sometimes lead to the conclusion that the males are indiscriminate. For example, when encounter rates with females are relatively low, the optimal selective strategy may appear indiscriminate (s versus r in Fig. 3b). Under the same conditions, although the learning strategy has the potential to increase selectivity over time in female population V_2 (from s towards a_{V_2} in Fig. 3b), the rate of learning (which is determined by external factors) is probably too low to produce measurable change (Fig. 4b) in mating success (Fig. 2 left bars).

We found relatively small overall advantage of learning under most of the conditions considered in spite of the fact that we deliberately chose a few parameters favouring learning. First, it is now established that learning is beneficial when there is some combination of long-term variation, which makes fixed strategies perform poorly, and short-term stability, which allows animals to reap the benefits of learning before changes occur (Stephens 1991; Dukas 1998). We therefore assumed that males were born into either of two populations, each including mostly sexually unreceptive females and a small proportion of sexually receptive females. On the one hand, the long-term variation was achieved by assigning each male to either of the two populations, in which the sexually receptive females had average pheromone signal either similar to or distinct from the sexually unreceptive females (Fig. 1). On the other hand, the short-term stability was created by assuming no change during a male's lifetime. One can readily imagine other situations in which the potential benefit from learning would be lower.

Another assumption that could magnify the relative benefits of learning was no learning costs. Learning must have costs associated with extra brain tissue devoted to learning and memory, and the physiological maintenance of memories (Dukas 1998, 1999). Indeed, significant costs of learning have been quantified in fruit flies (*D. melanogaster*) (Mery & Kawecki 2003, 2004, 2005). However, we currently do not have sufficient information for assigning a given cost to learning in the context of courtship. Moreover, such arbitrary cost assignment will not alter our model's conclusions, which agree with the empirical data indicating the occurrence of learning in the context of courtship in male fruit flies (Siegel & Hall 1979; Dukas 2005; Ejima et al. 2005). That is, we can probably conclude that learning in the context of courtship is slightly less beneficial than presented here but that it is sufficiently advantageous to be maintained at least in some insects.

Although our above assumptions favoured learning, other assumptions were either neutral or reduced the relative value of learning. Most notably, the null model

of selectivity was based on perfect knowledge of female pheromonal distributions over many generations, which allowed us to calculate an efficient optimal innate strategy (see, for example, s_{V_2} versus a_{V_2} in Fig. 3c). Making the selective strategy less efficient would increase the potential value of learning under some conditions. However, because the selective strategy is the starting point of the learning strategy, the actual relative performance of learning may be higher only under some settings that allow rapid learning (see examples in Fig. 4). Finally, it is possible that we have not considered some realistic parameter combinations that confer large advantages of learning. Future studies can readily evaluate such settings by running simulations of our general model with empirically derived parameters for a certain species.

Are Insects Bayesian?

We used a conventional technique involving Bayes' Theorem to model the learning strategy (Stephens & Krebs 1986; Luttbegg & Warner 1999; Clark & Mangel 2000; Uehara et al. 2005). It is thus pertinent to ask whether animals in general, and insects in particular, are able to compute algorithms similar to the Bayesian approach. The two fundamental features of the Bayesian approach are, first, the notion of prior and posterior knowledge, and, second, the concept of conditional probability density functions. It is well established that animals, including insects, possess prior, or innate, knowledge, which they may update with experience. For example, honeybees, *Apis mellifera*, have an innate template indicating that the sun sets opposite of where it rises and that it crosses from the rising to setting halves of the sky by midday. Bees update this general template with experience to represent the actual pattern of solar movement (Dyer & Dickinson 1994; Dyer 2002).

In the context of courtship, male fruit flies (*D. melanogaster*) appear to have innate knowledge about the expected pheromonal composition of various categories of females. For example, male fruit flies spend much more time courting virgin, sexually receptive females than recently mated, less receptive females (Cook & Cook 1975). Male fruit flies, however, can also update their prior knowledge with experience (Siegel & Hall 1979; Dukas 2004, 2005). We should note that the courtship conditioning protocol commonly used in neurogenetic laboratories (Siegel & Hall 1979; Connolly & Tully 1998, page 314) indicates that male fruit flies learn to reduce courtship of anaesthetized virgin females after unsuccessfully courting recently mated females. We believe that this nonintuitive result is caused by the use of immobilized, anaesthetized females. This is because males do not reduce courtship of freely moving virgin females after courting unsuccessfully recently mated females (Dukas 2005).

It is currently unknown whether the brain of any species represents information as conditional probability density functions. A few studies suggest that human perception is consistent with performance optimizing Bayesian rules (Fiser & Aslin 2002; Kording & Wolpert 2004) but the underlying neuronal processes have not

yet been examined (Knill & Pouget 2004). It is possible that insects and other animals use some statistical decision rule that is simpler than the Bayesian process we have modelled. This issue requires further investigation.

Conclusions

Our analyses indicate the conditions that would favour learning in the context of courtship compared to realistic nonlearning alternatives. Learning is favoured over indiscriminate courtship when either encounter rates with females are high or courtship durations are long. Learning is favoured over innate selectivity when encounter rates with females are high, when there is a large proportion of sexually receptive females and when the acceptance rate by sexually receptive females is high. We suggest that insect species in which such conditions commonly occur are most likely to show learning in the context of male courtship.

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Appendix

We use the set-up in Clark & Mangel (2000, page 239):

$$\Pr(\mu = \mu_j) = p_j (\text{Prior distribution}).$$

The male has two sources of information that can be used to learn about the current value of the mean pheromone signal of sexually receptive females, μ_V . (We assume that the proportion of sexually receptive files, λ , is fixed.) First, if the male encounters higher pheromone levels x , on average, than expected, he infers that μ_V is larger than normal (and vice versa). Second, if, for a given x , the male is accepted more often than expected, he infers that μ_V is closer to x than expected. We use Bayes' theorem in both cases.

Updating Based on the Pheromone Levels of Females Encountered

$$p'_j = \Pr(\mu = \mu_j | x) = \frac{\Pr(x | \mu_j) p_j}{\sum \Pr(x | \mu_k) p_k}, \quad (\text{A1})$$

where

$$\Pr(x | \mu_j) = \Pr(V) \Pr(x | \mu_j, V) + \Pr(N) \Pr(x | \mu_j, N) = \lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x) \quad (\text{A2})$$

The p'_j are the posterior probabilities, but become the prior probabilities for the second updating (if the male decides to court).

Updating Based on the Courtship Outcome

The male has observed x , updated the p_j , and decides whether to court (using $\bar{\mu}' = \sum p'_j \mu_j$, the posterior average of μ). If he does not court, there is no further updating. If he does court, the updated p''_j depends on the outcome:

$$p''_{j,\text{acc}} = \Pr(\mu = \mu_j | \text{accepted}) = \frac{\Pr(\text{acc} | \mu_j) p'_j}{\sum \Pr(\text{acc} | \mu_k) p'_k},$$

where, with x now given,

$$\Pr(\text{acc} | \mu_j) = \Pr(\text{acc} | V) \Pr(V | \mu_j) + \Pr(\text{acc} | N) \Pr(N | \mu_j) = p_s \frac{\lambda f_V(x; \mu_j)}{\lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x)} \quad (\text{A3})$$

because

$$\Pr(V | \mu_j, x) = \frac{\Pr(x | V, \mu_j) \Pr(V)}{\Pr(x)} = \frac{\lambda f_V(x; \mu_j)}{\lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x)}.$$

By substitution, we conclude that

$$p''_{j,\text{acc}} = \frac{\frac{f_V(x; \mu_j)}{\lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x)} p'_j}{\sum_k \frac{f_V(x; \mu_k)}{\lambda f_V(x; \mu_k) + (1 - \lambda) f_N(x)} p'_k}. \quad (\text{A4})$$

For rejection, we have

$$p''_{j,\text{rej}} = \frac{\Pr(\text{rej} | \mu_j) p'_j}{\sum \Pr(\text{rej} | \mu_k) p'_k}, \quad (\text{A5})$$

where

$$\Pr(\text{rej} | \mu_j) = \Pr(\text{rej} | V) \Pr(V | \mu_j) + \Pr(\text{rej} | N) \Pr(N | \mu_j) = (1 - p_s) \frac{\lambda f_V(x; \mu_j)}{\lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x)} + \frac{(1 - \lambda) f_N(x)}{\lambda f_V(x; \mu_j) + (1 - \lambda) f_N(x)}. \quad (\text{A6})$$