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Bayesian mating decisions in an amphipod, *Gammarus lawrencianus* Bousfield

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Abstract. In *G. lawrencianus*, females of a given fecundity and proximity to copulation day are assessed by males to be more valuable as mates, the longer the males have amplexed with the females (i.e. the greater their past investment in the act of amplexus). This behaviour is consistent with the hypotheses that (1) males are uncertain of the true reproductive state of a female on first contacting her; (2) the prior distribution of unamplexed females likely to be encountered by the males affects their initial estimates of a female's state; and (3) the time spent amplexing with a female allows information to be gathered which reduces a male's uncertainty of the female's state.

In his analysis of parental investment, Trivers (1972) implied that, once embarked on a task, an animal should invest further simply to avoid wastage of past investment. Dawkins & Carlisle (1976), Boucher (1977) and Maynard Smith (1977) rejected this on theoretical grounds, stressing that decisions should be made on the basis of future returns and the cost of completing the task, but not the degree of past investment. As a result of this theoretical exchange, Trivers' argument is now widely known as the 'Concorde fallacy'.

Two field studies, one by Weatherhead (1979) on savannah sparrows and another by Dawkins & Brockmann (1980) on digger wasps (*Sphex ichneumoneus*) put the issue to empirical test. Both species appeared to behave in a Concordian fashion, and the authors were left with post hoc explanations of the apparent failure of natural selection to 'optimize' behaviour. Faced with this possible conflict between observation and theory, we investigated the effect of past investment on decision-making in a gammaridean amphipod, *Gammarus lawrencianus* Bousfield. In so doing, we considered the possibility that past investment (in the sense of time 'invested' in a task) might be expected to influence decision-making by affording the opportunity for information pertinent to the decision to be gathered, and hence for uncertainty to be decreased. With decreased uncertainty, the animal's estimate of the future returns to be derived from completing the task might change. In investigating the effect of uncertainty on decision-making, the appropriate approach is a Bayesian analysis (Raiffa & Schlaifer 1961).

Gammarus lawrencianus is a euryhaline estuarine amphipod occurring from Labrador to Long Island Sound (Steele & Steele 1970). Because of its hardiness in the laboratory and short generation time, we have used it to examine phenotypic and genotypic correlations among life-history traits (Doyle & Hunte 1981a, b; Doyle & Myers 1982).

Males of *G. lawrencianus* attempt to hold any females that their antennae contact; after examination they either reject or accept them. Acceptance is indicated by the male carrying the female with him for about 4 days prior to her becoming ready for copulation; this precopulatory carrying stage is known as amplexus. The pairing behaviour of *G. lawrencianus* does not differ qualitatively from that described for *G. pulex* and *G. fossarum* by Ducruet (1973) and for *G. duebeni* by Hartnoll & Smith (1978). At copulation, the female passes the fertilized eggs forward to a thoracic brood chamber where they remain until hatching, which occurs just prior to the next copulation. The amplexed pair separates immediately following each copulation. Females do not store sperm, and there is no indication that being amplexed accelerates the rate at which females become ready for copulation.

During the period of examination occurring when a male first holds a female, the female typically lies passively in a curled position. In this case, we view the decision of whether or not to amplex as reflecting a choice by the male. In certain circumstances, specifically when females are large relative to the males attempting to hold them, the females straighten and flex their abdomens vio-

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lently during male examination, finally freeing themselves from the males and swimming off alone. We view this as reflecting a choice by the female. That mate choice by males is a predominant feature of the mating system of *G. lawrencianus* is presumably a reflection of the large male investment in each reproductive act necessitated by amplexus (Bateman 1948; Trivers 1972; Williams 1975).

In the present study we used only males and females whose relative sizes ensured that we were operating within the size ranges over which male choice prevails. The rejection or acceptance of a female by a male is based primarily on two criteria. The first is the proximity of the female to copulation day (subsequently referred to as female State). Early amplexing increases the cost of carrying and possibly the risk of predation (Strong 1973), and lowers the encounter rate with other females. The second criterion is the female's size relative to the male's. Female fecundity is proportional to size, but the larger the female the higher the probability of her being taken by other males, and presumably the higher the energetic cost of carrying her. These aspects of the mating system of *G. lawrencianus* will be further dealt with in a subsequent publication.

METHODS AND RESULTS

The Effect of Past Investment on Male Mating Decisions

All experiments were conducted at 22 C, and the animals were observed continuously throughout each experiment. We used males and females of similar sizes (19·0–20·0 mg for males; 9·0–10·0 mg for females), thus standardizing the number of fertilized eggs obtained by the male should copulation be achieved. We use the concept of 'value' of a female to a particular male in the context of the criteria of female acceptability outlined above. We investigated how a male's assessment of female value was affected by (1) the amplexus time remaining to copulation (female State), and (2) for a female of a given State, the amplexus time already committed to the female (i.e. the past investment committed to the amplexus).

We assumed that we could measure the male's assessment of female value by measuring the amount of time that he would endure stress before releasing the female from amplexus. The stress we used was exposure to low salinity, which is a common occurrence in the natural habitats of animals living in the intertidal zone of estuaries (Southward 1965). The males were exposed to stress by placing the amplexed pair in distilled water and measuring the time that elapsed before the female was released (i.e. time to separation). To allow for variation in tolerance to salinity stress, males were left in distilled water after separation and the time to succumb was measured. A male was considered as having succumbed when he was unable to right himself (Doyle 1978). Once the male had succumbed, he was placed in brackish water and allowed to recover. We call the ratio Time-to-Separation/Time-to-Succumb a Tenacity Index, and assume that it reflects a male's assessment of the female's value.

To investigate how the Tenacity Index was affected by female State and by the time already committed to amplexus, we conducted two experiments, termed respectively Continuous Amplexus and Interrupted Amplexus. We placed animals together in a 40-litre stock tank and allowed them to amplex. In most cases, amplexus occurred when females were 4 days from copulation, and only such pairs were used in the two experiments. Amplexed pairs were immediately removed from the stock tank and kept in individual containers (1-litre 'Tupperware' containers). Each pair was removed by placing under it a small 'platform' of semi-rigid mesh, lifting the platform up, and transferring the pair immediately to the appropriate container.

In the Continuous Amplexus experiment, the Tenacity Index was measured on the day of amplexus and on days 3, 2, 1 and 0 preceding copulation. This corresponds to female States 4, 3, 2, 1 and 0, respectively, a female in State 0 being one which is ready to copulate on that day. A total of 63 pairs were used in the experiment, each pair being used only once. There is a positive linear relationship between Tenacity Index and time since initially amplexing (Fig. 1, Continuous Amplexus: $y = 0{\cdot}357 + 0{\cdot}150x$; $b_1 > 0$, $F = 90{\cdot}3$, $P < 0{\cdot}001$). Since there was no significant relationship between time to succumb and time spent amplexing, this result superficially suggests that there is increasing value placed by males on females as the latter approach copulation. However, it is not only female State that is changing, but also the time that the male has already spent amplexing with the female.

In the Interrupted Amplexus experiment, the individuals of a pair were separated by gentle manipulation 3 h after removal from the stock tank, and were kept separately in individual containers. The members of each pair were allowed to re-amplex 6 h prior to being tested for tenacity. The Tenacity Index was measured when females were in States 4, 3, 2, 1 and 0, as above. Seventy-four pairs were used in the experiment, each pair being used only once. Again, there is a positive relationship between Tenacity Index and time since initially amplexing (Fig. 1, Interrupted Amplexus: $y = 0{\cdot}309 + 0{\cdot}117x$; $b_2 > 0$, $F = 118{\cdot}5$, $P < 0{\cdot}001$). This confirms that females are valued more highly by males as they approach copulation, since the time that the male had spent amplexing with the female was held constant in this experiment. Both the Continuous Amplexus and the Interrupted Amplexus experiments were subsequently repeated by a technical assistant, in a double-blind experimental design, and the results obtained were consistent with the original experiments.

The intercepts of the lines in Fig. 1 do not differ significantly ($t = 0{\cdot}189$, $P > 0{\cdot}10$), but the slopes do ($b_1 > b_2$; $t = 3{\cdot}11$, $P < 0{\cdot}005$). This suggests that a male which has amplexed longer with a female of a given State values her more highly (i.e. a male's past investment in a particular female is affecting his assessment of her value). This difference in the male's assessment of female value can be expressed in units of male amplexing time. A female in State 0 who has been in continuous amplexus (i.e. 4 days of amplexing) is valued more highly than a State 0 female only just amplexed, by the equivalent of 29·5 h of male amplexing time (Fig. 1). In short, the male apparently estimates that the latter female will require 29·5 h more amplexing time than the former before she will be ready for copulation.

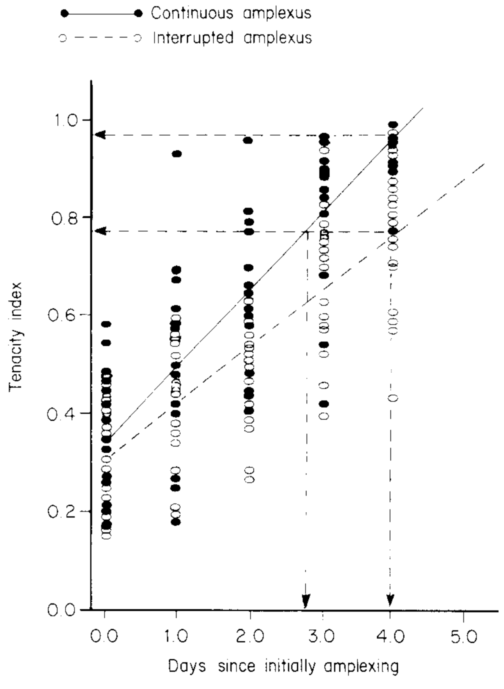

Figure 1. Tenacity Index as a function of days since initial amplexus, given separately for interrupted and continuously amplexing males. For Continuous Amplexus, $y = 0{\cdot}357 + 0{\cdot}150x$ ($b_1 > 0$, $F = 90{\cdot}3$, $P < 0{\cdot}001$). For Interrupted Amplexus, $y = 0{\cdot}309 + 0{\cdot}117x$ ($b_2 > 0$, $F = 118{\cdot}5$, $P < 0{\cdot}001$).

The Effect of Uncertainty on Male Mating Decisions: Bayesian Decision-making

One reason why females of a given State may be valued differently depending on the time that the male has been amplexing with them is that males may be uncertain of the true State of females on first amplexing.

It seems likely that following the onset of amplexus, a male gathers information about a female which allows him to assess her State with increasing accuracy as time passes. This is made more credible by our observation of the male's behaviour at amplexus. The dorsal surface of the female's abdomen is encircled by the ventral surface of the male's and is rubbed vigorously, while the female is frequently turned at right-angles to the male and her ventral thoracic surface probed by the male's gnathopods. This behaviour is repeated with decreasing frequency on the days following the onset of amplexus. Thus the longer a male has been amplexing, the more certain he may be of the female's State.

To investigate the effect of uncertainty on decision-making, it is necessary to quantify the degree of uncertainty prevailing. We attempted to do this for a male's uncertainty of a female's State when he first encountered her. We placed males individually in 17 containers, each holding 15 females. In each container all females were in the same State. Containers were set up with females ranging in States from those at 7 days to copulation to those on their copulation day. Each male was left in a container for 6 h and was scored as having accepted a female if he was amplexing at the end of this period. A total of 340 males were used in the experiment. The results are shown in Fig. 2 as

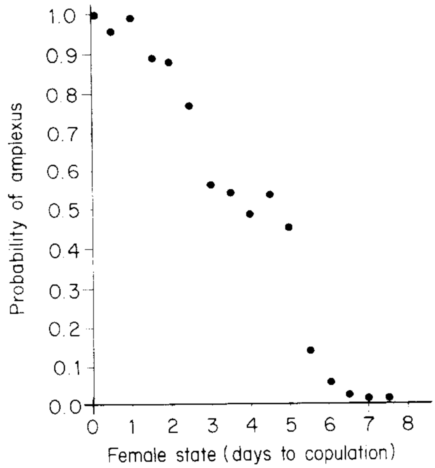

Figure 2. Probability of a female being amplexed as a function of female State (days to copulation).

probability of acceptance versus female State (where probability of acceptance is considered synonymous with percentage acceptance). Females at 4 days to copulation were amplexed with a probability of 0·48, and State-3 and State-5 females were amplexed with similar probabilities after the 6 h of contact time (Fig. 2). We therefore chose 1 day on either side of a female's true State as being the region over which a male is uncertain of a female's State on the first encounter.

But why should male uncertainty on first amplexing cause males to underestimate the State of females, as suggested (see Fig. 1) by our results? In attempting to assess a female's State at the first encounter, a male has two sources of information. The first source, which is known before the particular female is contacted, is the distribution of States of unamplexed females in the population (i.e. the prior distribution of unamplexed females). This could be 'known' as a component of the male's genotype or, as more likely in this case, be generated by the continuous sampling of the female population by males. The second source of information is the male's observation of the particular female on first contacting her.

Let $p(x_i)$ be the probability that an unamplexed female encountered is in state x_i. We determined this 'prior' probability by investigating the distribution of x_i (i.e. female States) among non-amplexed females in a laboratory population of sex ratio 1:1. This distribution is shown in Fig. 3. The sharp decrease in availability of State-4 and State-3 females reflects the fact that males typically amplex with females about 4 days prior to copulation. After copulation, females typically re-enter the non-amplexed female population as State-7 females. The point to appreciate is that male uncertainty at the time of first amplexing, along with this distribution of States of non-amplexed females, can cause an underestimation of the female's true State on first encounter.

Consider a male who has information on the distribution of the States of unamplexed females (his first information source; Fig. 3) and who encounters a female whose true State is x_i. The male makes an observation, h, of the female's State. This observation might be based on one or more of several possible cues that the male could use to assess female State. For example, it might be the texture or stiffness of her exoskeleton, since females moult at every copulation. The conditional probability of the male making observation h, if the female's true State is x_i, is $p(h|x_i)$. This conditional

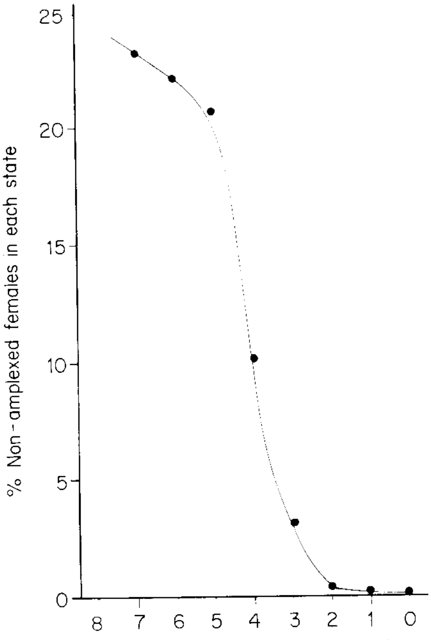

Figure 3. The distribution of non-amplexed females in the population as a function of female State (days to copulation).

probability is the male's second information source, which is obtained on actual contact with the female.

Bayes' theorem specifies the way in which an 'ideal' observer would combine the two sources of information to generate a final posterior probability distribution of female States. In short, we can calculate the probability that the females encountered would be in State x_i given the distribution of female States and that the male has made observation h. To do this, we assume a uniform distribution for $p(h|x)$, i.e. we assume that on first contact the male determines the female State within some range (probably ± 1 day, in this case), but is unable to distinguish between female States within this range. That is, if the true State of a female is x_t, then

$$p(h|x) = \frac{1}{2a} \text{ if } x-a \leq x_t \leq x+a$$

$$= 0 \text{ otherwise.}$$

The posterior probability is written as $p(x_i|h)$, and is calculated as

$$p(x_i|h) = \frac{p(h|x_i)\,p(p_i)}{\sum_i p(h|x_i)\,p(x_i)}$$

This is Bayes' theorem (Raiffa & Schlaifer 1961). The prior distribution, $p(x)_t$ is empirically described by a cubic spline function (de Boor 1978) fit to the observed points in Fig. 3. The resulting posterior distribution, $p(x|h)$ is then determined by numerically performing the integration in Bayes' theorem. Hence for each true female State and for each uncertainty range, a posterior distribution of female States can be generated. Since it is more convenient to work with a single number than a distribution, we have plotted the expectation for female States over the posterior distribution for a number of true female States and for different ranges of male uncertainty (Fig. 4). The 'Bayesian estimate' of female State in Fig. 4 is thus $\int xp(x|h)\,dx$. With a male uncertainty range of ± 1 day, the State of a recently amplexed female on copulation day would be underestimated by about 23 h and 30 min.

Thus the effect of male uncertainty and of the prior distribution of female States is large enough to substantially account for the observation that recently amplexed males apparently assess State 0 females as requiring 29·5 h of amplexing time before they will be ready for copulation.

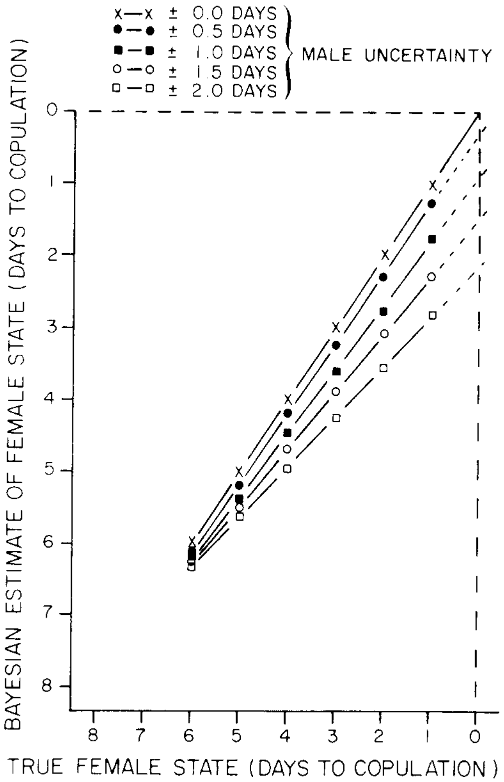

Figure 4. Male estimates of female States (i.e. Bayesian estimates which allow for the impact of prior probabilities) versus true female States for a range of male uncertainties of female State at the start of amplexus.

DISCUSSION

Decision-making processes cannot be understood without appreciating the selective pressures that shape them (McFarland 1977). Less often emphasized is that decision-making may remain obscure if we fail to consider constraints on the realization of optimal choices. Arguments that decisions should be made on the expectation of future returns and the cost of completing the task, but not on the degree of past investment, are sound (e.g. Dawkins & Carlisle 1976; Boucher 1977; Maynard Smith 1977). However, decisions are probably seldom made with perfect knowledge. Hence past investment, in the sense of time 'invested' in a task, may often influence an animal's estimates of the future returns to be derived from completing the task, since it may afford the opportunity for relevant information to be accumulated. For example, Oaten (1977), in the context of foraging in patches, has suggested that it could pay to behave in an apparently suboptimal manner in the first few patches, by staying longer in them, so as to have better estimates of resource distribution for use in later patches.

'Optimal' choices will clearly be constrained by the rate at which relevant information can be gathered and the time available to gather it. The importance of information-gathering in habitat selection has been considered by Doyle (1975), who showed that it can explain the steady decrease in 'choosiness' of planktonic larvae with time spent in the plankton. Maynard Smith & Parker (1976) and Parker & Rubenstein (1981) have investigated the acquisition of information in animal contests.

The effect of uncertainty on decision-making may be even more pronounced if, as in the present study, the animal has prior information about the resource likely to be encountered. Our observations of mating behaviour in *G. lawrencianus* are consistent with the hypothesis that the prior distribution of female States markedly affects a male's assessment of the State of a female that he has contacted. It seems likely that in the majority of decision-making situations in nature, an animal will possess prior information, at the time of the decision, that may affect the choice made. The present study suggests that these effects may be appreciable. However, this aspect of decision-making has received negligible empirical attention, possibly because of the difficulty of quantifying its effect in nature. We know of no studies, apart from those on man, which have empirically investigated the effect of information gathering and the impact of prior probabilities on decision-making; but Iwassa et al. (1981) have considered prior information in their theoretical treatment of foraging in patches.

Human subjects consistently exhibit 'conservatism' in decision-making: i.e. when supplied with new information, the difference between their revised (posterior) probabilities and their prior probabilities is consistently less than prescribed by Bayes' theorem (Philips & Edwards 1966). Should *G. lawrencianus* exhibit similar conservatism, the underestimation of female values that we calculated for recently amplexed males would be even greater. Our calculated underestimation does fall marginally short of the observed value in *G. lawrencianus*, which is consistent with observations on human decision-making.

In concluding, we stress that 'optimal' decisions depend on the information available to the animal, which may differ significantly from that available to the scientific observer. An analysis of decision-making in the presence of uncertainty requires a knowledge of the degree of uncertainty an animal has of the particular resource about which the decision must be made, and also a knowledge of the prior information that is available to the animal about the distribution of resources. Moreover, many organisms may be incapable of producing ideally revised posterior probabilities, as is apparently the case with humans and *G. lawrencianus*.

Given the magnitude of the effect of prior information on decision-making in the present study, it seems likely that these complications will have to be addressed for a fuller comprehension of decision-making in nature.

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