around the piece of leaf on which they are feeding (e.g., Carroll and Hoffman 1980). However, behavioural adaptations that prevent the transmission of induced defences beyond the damaged leaf have not been demonstrated. It is clear that field and laboratory experimentation will be required to test the ideas presented in this paper. If our hypothesis is proved correct, it will provide an important new dimension to the understanding of insect-plant interactions.

References

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On multiple mating and female fitness: comments on Loman et al. (1988)

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The occurrence of multiple mating by females has generated numerous explanations of the evolution of the behaviour (e.g. Halliday and Arnold 1987). One such explanation is the possible female benefits derived from producing a more genetically diverse set of offspring (Pease 1968, Williams 1975, Walker 1980, Thornhill and Alcock 1983, Halliday and Arnold 1987). This notion, although theoretically possible, has been criticised and is still controversial (e.g. Williams 1975, Walker 1980, Knowlton and Greenwell 1984, Parker 1984). Loman et al. (1988) recently published a model “demonstrating that female multiple matings, and thus increased genetic heterogeneity within a brood, can result in increased female fitness”. The model assumes that males are either “good” or “bad” as mates for specific females. Given this and several other assumptions Loman et al. (1988) suggest that the model may explain multiple matings by females in species where males provide nothing but their gametes in mating. I will argue that the model does not properly apply to the current discussion of offspring genetic diversification as a possible benefit for females in multiple matings, and that the model concerns potential female benefits only, rather than effect on female fitness in mating multiply.

The queen of evolutionary problems versus multiple mating

Though certain similarities exist, a distinction has to be made between (1) the differences in offspring genetic diversity in sexually (recombimational) and asexually (non-recombinational) reproducing organisms on one hand, and (2) the differences in offspring genetic diversity in single- and multiple-mated females of a sexually reproducing organism on the other. In the first case most scientists agree that there is a tremendous difference in genetic diversity of offspring mostly due to recombinational processes (see Stearns 1987 for a recent review). This difference forms the basis for most of the potential benefits involved in sexual reproduction (e.g. Ghiselin 1974, Williams 1975, Maynard Smith 1978, Bell 1982, Stearns 1987). In the second case, the difference in offspring diversification is of a completely different order of magnitude. As a matter of fact, Williams (1975) holds that one mating is often sufficient to provide a genetic within-progeny diversity that halts that of the whole population. Thus, mating with only a few males may often provide a female with an almost maximal genetic diversity of her offspring (Williams 1975). Considering these relationships, it is obvious that the “queen of problems in evolutionary biology” (the evolution of sex; Bell 1982) is widely separated from the occurrence of multiple mating by females. Further, models dealing with sexual selection have quite different explanations for the twofold cost of sex (Bell 1984, Lewis 1987). This may create confusion (cf. Loman et al. 1988).

Benefits derived by offspring diversification

Models concerning female multiple matings mainly focus on increased genetic diversity (cf. sexual selection; Williams 1968, 1969, Williams 1975, Bell and Alcock 1983, Knowlton and Greenwell 1984). Benefits of offspring diversification in single mating are incorporated. Potential adaptations of diversification in itself depends on the mechanisms on offspring diversification in varying environments. Different species with e.g. parasites (Maynard Smith 1978, 1979, Bell 1982, Stearns 1987) and beneficial bacteria (Williams 1975) “ensure” that the essential genetic diversity is incorporated (e.g. “the bacteraeal variety based on the recognition of diversely different environments”) of different offspring (see Loman et al. 1988). In environmental conditions, Loman et al. (1988) suggest that processes on viable offspring diversification of the number of viable offspring and the genetic diversity of the viable offspring is a function of the environmental conditions. Since these are basic (the current model is based on the problem of offspring diversification; given above) neither the diversification of offspring diversification is a function of the environmental conditions. Further, in their model Loman et al. do not consider potential benefits by reduced density and the proportion of the mating population (e.g. effect sterile or almost sterile). For these reasons I question the plausible nature of this diversification.
models dealing with the evolution of sexual reproduction have quite different prerequisites (e.g. balancing the twofold cost of sex; Williams 1975, Maynard Smith 1984, Lewis 1987). These conditions imply that models concerning the two different problems should not be confused (cf. Loman et al.: 71).

Benefits derived by offspring diversification

Models concerning female multiple matings suggest that multiple matings may be a female strategy to further diversity (cf. sexual reproduction) of offspring (Pease 1968, Williams 1975, Walker 1980, Thornhill and Alcock 1983, Knowlton and Greenwell 1984). The potential benefits are thought to be the same as for sexual reproduction itself, though of a different magnitude (cf. above). The general theoretical problem is: does the genetical diversification of offspring represent a benefit, and if so, what are the selective regimes favouring offspring diversification? In discussing the possible benefits of diversifying the genetical composition of offspring, no aspect of universal male genetical quality is incorporated. Potential benefits are derived by the very diversification itself, mediated by different selective mechanisms on offspring, e.g. unpredictable or varying environments, different competition or evolutionary races with e.g. parasites (Ghiselin 1974, Williams 1975, Maynard Smith 1978, 1984, Hamilton 1980, Walker 1980, Bell 1982, Stearns 1987). The models (including Williams’ (1975) “elm-oyster model”) are generally based on the recognition that a diverse (or heterogeneous) set of offspring may be beneficial, since the fitness of different offspring genotypes differs under various environmental conditions. In contrast, the model of Loman et al. (1) does not involve any selective processes on viable offspring (e.g. “...a critical variable is the number of viable offspring...”) and (2) assumes that the viable offspring is not diverse and that the fitness of all viable offspring is the same (e.g. “...For the purpose of this model all viable offspring are equally fit.”). Further, a very large variance in male basic genetical quality is assumed (e.g. “...There is a large variation in male suitability when mating with a particular female.”). Since these are basic assumptions, the model of Loman et al. does not correspond to the current discussion of the problem of offspring diversification (cf. references given above). Neither does it represent female benefits from offspring diversification of heterogeneity sensu strictu.

Further, in their evaluation, females receive most notable benefits by mating multiply when a very large proportion of the males (80%) are “bad males” (in effect sterile or almost sterile to females; 0-20% offspring viability). For reasons of evolutionary dynamics, I question the plausibility and universality of such situations.

The nature of genetical differences between males

The effect on female fitness of multiple matings in terms of increased offspring genetical diversity is very difficult to assess and thus controversial (e.g. Williams 1975, Walker 1980, Knowlton and Greenwell 1984, Parker 1984). As recognized e.g. by Williams (1975), Walker (1980) and Knowlton and Greenwell (1984), the magnitude of the potential benefits largely depends on the magnitude and nature of the genetic variance within the population. That is, the higher genetical variance and the greater the additive component is in this variance, the greater should the potential benefits of multiple matings be to females. Thus, when developing a model to evaluate potential benefits to females in mating multiply, male genetical variance is critical to the outcome. This has not been taken into consideration by Loman et al., by simply assuming a very large and conservative male genetical variance (0 vs 100% and 20 vs 80% offspring viability).

The cost of mating and female fitness

When considering the possible effects of a certain behaviour on fitness, both costs and benefits should be considered. When modelling the possible effects on female fitness derived from mating multiply, one should thus incorporate the costs of mating. The potential costs of mating may be summarized as: (1) time and energy costs devoted to courtship and copulation, (2) increased risk of predation while mating, (3) risk of injury inflicted by the male and (4) risk of disease or parasite transmission (see reviews by Daly 1978, Thornhill and Alcock 1983, Lewis 1987). In their model, Loman et al. assume (implicitly) that matings are costless to females. If matings involve costs to females, the cost of mating will increase with the number of matings and thus be of critical importance to the effect on female fitness of multiple matings (e.g. Daly 1978, Knowlton and Greenwell 1984). Since matings in most animal species are likely to involve at least some costs to females, the validity of the model of Loman et al. in terms of fitness is weakened (according to the model, a female mating e.g. with 5000 males will gain higher fitness than a female mating with 5 males). The model may thus be said not to concern the fitness of multiply mated females, but rather potential female benefits in mating multiply (cf. Loman et al. 1988, e.g. p. 71: “...the fitness is obtained by rewriting the latter part of Eq. 3a as: (Eq. (4))”).

Though the model developed by Loman et al. does not properly concern the effect of genetical diversification of offspring on female fitness, as I see it, it develops another possible benefit to females by mating multiply, namely to “hedge” against the probability of some males being sterile or genetically defective (Gibson and Jewell 1982, Halliday and Arnold 1987). The model may show that if inferior males are common and their
A better title: "Female benefits from multiple matings - a model"

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We realize, after having perused the note by Arnqvist (1989) that the title of our recent paper (Loman et al. 1988) was unfortunate. We did not discuss genetic heterogeneity in the conventional sense but operationally defined two genetically based offspring classes, “good” and “bad”. However, as each of these may be genetically quite diverse, we cannot make any assumptions about total genetic heterogeneity. We discussed effects on female fitness (defined below) from increasing the offspring diversity with respect to these two classes.

The purpose of the model was to demonstrate how female fitness is affected by multiple matings. Our definition of “fitness” was of course meant to simplify the presentation in this particular context. Many other factors might also have an impact on total female fitness. There might, for example, be costs associated with matings, which is one aspect of number of matings that might lower fitness. This is evident from the example concluding our paper. The fitness of an individual female naturally depends on all such contributing factors. One point where we disagree with Arnqvist is the

“plausibility and unlikelihood of a large proportion of viable offspring). We feel that this is very common. However, we believe that such theories of convergence are implausible. This is due to the fact that they are genetically incompatible. Our model shows that this may be important. This subject deserves

What is the advantage to females of gaining multiple mates? (17)

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It is likely that of the 500 species or so of Monarch butterflies (Danaus plexippus) that exists (Ehrlich 1985; Endler 1988), the number of colonies of predator-prey systems that involve distasteful monoploidy, that prey have predation. This single character has potential for misleading an evolutionary study.

At least five theorized adaptive anti-predator characters are involved: 1) Some charac- 2) A mimicry of心得 predation. tion. A complication is that these characters may function in addition to and in conjunction with each other. This problem is shared by all species of Monarch butterflies (Ehrlich and Kitchell 1987). The independent set of characters (e.g., mimicry, distastefulness, and defense; Ehrlich and Kitchell 1987), against avian predation, is a complex one that is less well understood.

The Monarch butterfly is a medium-sized, brightly-colored butterfly that relies on defense chemicals against avian predators. These chemicals can deter predators from consuming the butterfly. Some species of Monarch butterflies have developed a mechanism to sequester these chemicals from their food, which can be toxic to predators. This is an example of mimicry, where species that produce defense chemicals against avian predators have evolved to mimic each other's patterns. The Monarch butterfly is one of many species that use mimicry as a defense mechanism against predators.