

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 mate genetical quality is incorporated. Potential benefits are derived by the very diversification in itself, mediated by different selective mechanisms on offspring, e.g. unpredictable and/or varying environments, sib 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 stricto*.

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 defect (Gibson and Jewell 1982, Halliday and Arnold 1987). The model may show that if inferior males are common and their

genetical inferiority is severe enough, females may benefit from mating multiply under certain rather restrictive circumstances (though these benefits are not derived from mechanisms based on the genetical diversification of offspring *sensu strictu*). However, in such situations selection would favour (and very intensively so) mate quality rather than mate quantity (see Bateson 1978, 1980, Bateson et al. 1980, Partridge and Halliday 1984, for a discussion of inbreeding consequences and avoidance).

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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