

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).

Acknowledgements – I am indebted to C. Otto and K. Leonardsson for discussion and criticism of the manuscript.

References

- Bateson, P. P. G. 1978. Sexual imprinting and optimal outbreeding. – *Nature*, Lond. 273: 659–660.
- 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. – *Z. Tierpsychol.* 53: 231–244.
- , Lotwick, W. and Scott, D. K. 1980. Similarities between the faces of parents and offspring in Bewick's swans and the differences between mates. – *J. Zool.* 191: 61–74.
- Bell, G. 1982. The masterpiece of Nature: The evolution and genetics of sexuality. – Univ. of California Press, Berkeley, CA.
- Daly, M. 1978. The cost of mating. – *Am. Nat.* 112: 771–774.
- Ghiselin, M. T. 1974. The economy of nature and the evolution of sex. – Univ. of California Press, Berkeley, CA.
- Gibson, R. M. and Jewell, P. A. 1982. Semen quality, female choice and multiple mating in domestic sheep: a test of Trivers' sexual competence hypothesis. – *Behaviour* 80: 9–31.
- Halliday, T. and Arnold, S. J. 1987. Multiple mating by females: a perspective from quantitative genetics. – *Anim. Behav.* 35: 939–941.
- Hamilton, W. D. Sex versus non-sex versus parasite. – *Oikos* 35: 282–290.
- Knowlton, N. and Greenwell, S. R. 1984. Male sperm competition avoidance mechanisms: The influence of female interests. – In: Smith, R. L. (ed.), *Sperm competition and the evolution of animal mating systems*. Academic Press, New York, pp. 61–84.
- Lewis, W. M. 1987. The cost of sex. – In: Stearns, S. C. (ed.), *The evolution of sex and its consequences*. Birkhäuser, Basel, pp. 33–58.
- Loman, J., Madsen, T. and Håkansson, T. 1988. Increased fitness from multiple matings, and genetic heterogeneity: a model of a possible mechanism. – *Oikos* 52: 69–72.
- Maynard Smith, J. 1978. The evolution of sex. – Cambridge Univ. Press, Cambridge.
- 1984. The ecology of sex. – In: Krebs, J. R. and Davies, N. B. (eds), *Behavioural ecology*. Blackwell, Oxford, pp. 201–221.
- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. – In: Smith, R. L. (ed.), *Sperm competition and the evolution of animal mating systems*. Academic Press, New York, pp. 1–60.
- Partridge, L. and Halliday, T. 1984. Mating patterns and mate choice. – In: Krebs, J. R. and Davies, N. B. (eds.), *Behavioural ecology*. Blackwell, Oxford, pp. 222–250.
- Pease, R. W. 1968. The evolution and biological significance of multiple pairing in Lepidoptera. – *J. Lepid. Soc.* 22: 197–209.
- Stearns, S. C. (ed.) 1987. *The evolution of sex and its consequences*. – Birkhäuser, Basel.
- Thornhill, R. and Alcock, J. 1983. *The evolution of insect mating systems*. – Harvard Univ. Press, Cambridge, MA.
- Walker, W. F. 1980. Sperm utilization strategies in nonsocial insects. – *Am. Nat.* 115: 780–799.
- Williams, G. C. 1975. *Sex and evolution*. – Princeton Univ. Press, Princeton, NJ.

A better title: "Female benefits from multiple matings – a model"

Jon Loman and Thomas Madsen, Dept of Ecology, Animal Ecology, Univ. of Lund, Ecology Building, S-223 62 Lund, Sweden

Thomas Håkansson, Dept of Cultural Anthropology, Univ. of Uppsala, S-752 20 Uppsala, Sweden

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 universality” of situations where a large proportion of males are “bad” (producing unviable offspring). We agree that it seems unlikely to be very common. However, we do not know of data or theories that convincingly show such a situation to be implausible. This is especially true if some males are genetically incompatible with respect to certain females. Our model shows that such a situation might be important. This subject deserves further study.

In conclusion, and with some afterthought, a better title would have been the one heading this note.

References

- Arnqvist, G. 1989. On multiple matings and female fitness: comments on Loman et al. (1988). – *Oikos* 54: 248–250.
Loman, J., Madsen, T. and Håkansson, T. 1988. Increased fitness from multiple matings, and genetic heterogeneity: a model of a possible mechanism. – *Oikos* 52: 69–72.

What is the adaptive significance of multicomponent defensive repertoires?

David L. Pearson, Dept of Zoology, Arizona State Univ., Tempe, AZ 85287, USA

It is likely that of the vast majority of prey species each exhibits multiple anti-predator characters (Pearson 1985, Endler 1988). However, most models and theories of predator-prey interactions assume, at least implicitly, that prey have only single anti-predator characters. This single character assumption has great potential for misleading and invalid results.

At least five theories predict the presence of multiple anti-predator characteristics within a single individual prey: 1) *Some characters may function in concert to minimize predation.* For instance, aposematic coloration and distasteful compounds are frequently associated. A complication with this category is that each of these characters may not effectively deter predation by itself, and if they only or usually function in combination, they may technically be considered one character. Monarch butterflies (*Danaus plexippus* L.) use an interdependent set of characters that include color, gregariousness and distastefulness for much of their protection against avian predators on the wintering grounds (Calvert et al. 1979). Tiger beetles (Cicindelidae) use body size, brightly-colored abdomens exposed in flight, and defense chemicals against robber fly predators. The percent deterrence by these characters is greatest for larger species with bright orange abdomens and benzaldehyde released from their defense glands (Pearson 1985). As each of these characters is eliminated from models presented to wild robber flies, the deterrent effect is reduced. Some characters such as large body size are more important by themselves than other single characters, but the greatest protection is derived from a combination of all three together. Smaller tiger beetle species rely on gregariousness together with orange abdomens and defense compounds (Pearson et al. 1988).

2) *Some anti-predator characters may be largely or uniquely targeted against each of the distinct foraging phases of a predator* (Endler 1986). Predator behavior can be divided into distinct stages such as search, pursuit, capture and processing (Holling 1966). Anti-predator characters like crypsis are primarily effective against the searching phase, rapid flight against the pursuit phase, chemical defense against the capture phase, and hard cuticle against the processing phase. An individual prey might have all these characters to adequately protect it from a single or different predators through all of its foraging phases.

3) *Increasingly potent lines of defense may be used as a predator overcomes the initial ones.* The primary lines of defense function regardless of whether or not the predator has been perceived by the prey, and they are likely to be energetically cheap (crypsis). The secondary lines are initiated by an encounter with a predator and are generally more energetically expensive (chemicals) (Robinson 1969, Rotheray 1986). The tropical fulgorid bug, *Fulgora laternaria* L., is camouflaged to match the large tree trunks on which it roosts during the daytime. If vertebrate predators such as a bird approach, the resting bug can then expose large eye spots on its hind wings. In addition it has a large hollow extension of cuticle that projects anteriorly beyond the head and resembles a lizard or snake head. Presumably a predator able to surmount each of these defenses in turn will then take a bite of the large sham head and end up with nothing but cuticle and air (Janzen 1983).

4) *Prey encountering several different types of predators may need a separate anti-predator character targeted at each predator* (Downes 1987).

This phenomenon is perhaps the most obvious mul-