Evolutionary biology

Sexual conflict and speciation

Sexual conflict occurs because males are selected to produce as many offspring as possible, even if this means lowering the overall reproductive output of individual females. A new model proposed by Gavrilets[1] suggests that strong asymmetries between males and females in the costs and benefits of mating will create runaway coevolution between the sexes, promoting rapid divergence between populations and hence speciation. This is an intriguing possibility, not least because it runs counter to existing models[2] which suggest that greater sexual conflict will result in males mating more indiscriminately, breaking down reproductive barriers between divergent populations. One reason for this difference is that the new model is based on the idea that females can avoid costs of mating if they are incompatible with some males, whereas we suggest that in reality this may rarely be the case.

Gavrilets' model[1] assumes a quadratic relation between female fitness and the proportion of the male population with which she is compatible (morphologically, physiologically or genetically). The shape of this relationship is not theoretically derived (as it might be), but is the simplest function under which there is an intermediate optimum proportion of compatible males. This relationship is based on observations suggesting that females experiencing unusually high or low mating rates may have reduced fitness[3], but such analyses must be treated with caution. Females are expected to be adapted to the number of matings they experience[4], even if this is a compromise between their optimal mating rate and that which males attempt to impose.

More significantly, most of the costs to females that Gavrilets sees as driving sexual conflict (such as predation, sensory exploitation, different costs of mating or seminal fluid toxicity)[1] are paid as a result of matings *per se*, and hence can only be prevented if matings themselves are avoided. However, if incompatibilities prevent mating, then males are expected to be able to determine rapidly whether a particular female is compatible. Hence incompatibilities that prevent mating between particular male and female phenotypes will simply result in males only attempting to mate with females with whom they are compatible, with no reduction in the number of matings or attempted matings to which each female is subjected.

This suggests that the potential for sexual conflict to promote divergence may be limited to species without the possibility of pre-copulatory mate choice, but in which there are still costs to being compatible with too many males. There may be examples of such species — for instance, broadcast spawners may suffer from polyspermy — but such cases are likely to be rare.

Although we question the generality of Gavrilets' model[1], it does indicate the potential for the different priorities of males and females to drive evolution of reproductive isolation. Perhaps rather than lumping so much biology together under the title 'sexual conflict', we need to consider the specific processes involved.

Tom Tregenza, Roger K. Butlin, Nina Wedell
School of Biology, University of Leeds,
Leeds LS2 9JT, UK
e-mail: gentbt@leeds.ac.uk

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Gavrilets replies — Tregenza *et al.* maintain that my model's predictions[1] run counter to the model of Parker and Partridge[2], but it is not straightforward to compare these two classes of model because of their inherent differences.

First, my model considers genetic divergence of allopatric populations, whereas the models developed in ref. 2 describe the evolutionary consequences of a secondary contact between populations that have already diverged: that is, they model reinforcement of reproductive isolation rather than its emergence. Second, Parker and Partridge[2] use an evolutionarily stable strategy framework with a set of fixed evolutionary options, whereas I model continuous coevolution of the sexes, during which evolutionary options are continuously changing.

In spite of these differences and contrary to the claim of Tregenza *et al.*, there is no contradiction in the predictions of both types of model. Parker and Partridge propose that mating conflict could be either a hindrance to isolation if 'male-win' scenarios prevail, or a facilitator if females tend to win — exactly as predicted by my model if coevolution is restricted. However, my model takes an additional step by considering the possibility of continuous coevolution of the sexes. In this case the prediction is that neither sex will win the sexual conflict, but rather that there will be a dynamic coevolutionary compromise.

Tregenza *et al.* question the generality of my model's assumption that females have an intermediate optimum mating rate, as well as the specific (quadratic) function I used to model the relation between a female's fitness and her mating rate: in fact, the model is well supported by insect[3] and other data[4,5], and the idea that excessive mating rates are bad for females is the essence of sexual conflict.

Inadequate mating rates are also detrimental[6]. Thus, with sexual conflict the optimum mating rate must be intermediate. As for the shape of the relation between female mating costs and mating rate, more data are indeed necessary. However, I do not anticipate that using functions more complicated than a quadratic one will affect my main conclusions[1].

Tregenza *et al.* suggest that, in most species, males will rapidly identify and attempt to mate only with those females with whom they are compatible, thus reducing the potential for sexual conflict to promote divergence. But even if the necessary 'indicators' of female compatibility should be readily available and the males smart enough to exploit them, in a polymorphic population different females will experience a variable number of matings. This will induce fitness differences and initiate runaway coevolution, resulting in genetic divergence of isolated populations. Although the model does not describe all the specific processes involved in sexual conflict, other weaknesses are not yet apparent.

S. Gavrilets
Department of Ecology and Evolutionary Biology,
Department of Mathematics, University of
Tennessee Knoxville, Tennessee 37996, USA

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