The dark side of sexual selection

A casual reader of the behavioural ecology literature might think that sexual selection provides boundless evolutionary benefits to females. Females can directly choose a mate, or let males establish their worth by fighting amongst themselves for the chance to mate. We know that males trade the advantages of being chosen as a mate against the energy loss and risk to their lives of competing with one another and signalling to females. In contrast, our understanding of the process from the female perspective is dominated by attempts to resolve the benefits that females derive from mate choice or from multiple mating. The idea that a single mating can decrease a female's lifespan, and each additional mating or refusal to mate further decreases her survival and fecundity has received attention from only a handful of researchers[1–4].

The hidden costs to females when males compete to mate can be understood in terms of conflict between the sexes in the way that reproductive success is optimized[5]. A competitive male that outsignals or outfights other males will mate with more females and thus sire more offspring, even if his actions lead to a reduction in each mated female's reproductive output. The higher the potential variance in male mating success, the more important sexual selection becomes, and the greater the likelihood that it will lead to the evolution of traits incidentally harmful to females[6]. Female mate choice is one, but by no means the only, female adaptation that results from competition between males for mates. How females balance the costs of courtship and harassment by males with those of mating (e.g. sperm toxicity[7] and vulnerability to predators[2]) is a crucial aspect of female ecology. Variation in female tendency to remate greatly influences the strength and form of sexual selection in a population.

Sexual selection stopped

In a new study[8], Holland and Rice employed an innovative experimental technique to examine the long-term costs of intersexual conflict. They recognized that enforcing monogamy in the naturally promiscuous fruitfly *Drosophila melanogaster* would effectively remove the opportunity for sexual selection, and thereby negate the importance of male competitive adaptation. Moreover, monogamy should result in selection against male attributes that harm the female, because a male's reproductive success now depends solely on her reproductive output rather than his ability to inseminate several females. Similarly, forms of female resistance, such as reluctance to mate, which reduce the couple's lifetime reproductive output, should be selected against. Other forms of resistance (e.g. to toxic sperm compounds) should experience relaxed selection, or be indirectly selected against. They tested these predictions in two replicate lines of flies in which monogamy was enforced, compared with two control lines in which three males competed to mate with each female.

After 34 generations of monogamy, males were less likely to harm females (from a reference stock) than were males from the control. Both reproductive rate and survival (after one mating) were significantly higher in females housed with males from the monogamy treatment. Male virulence to females therefore decreased following monogamy. Monogamous females died faster than control females when kept with control males, which suggests reduced resistance to male competitive adaptations and courtship. Generally, these results echo and extend Rice's[4] earlier demonstration that females suffer shorter lives when female resistance evolution is stopped but male competition is allowed to proceed.

Most interesting is the demonstration that, after 47 generations, monogamous populations had significantly greater net reproductive rates as a result of faster development (there were similar numbers of surviving progeny per female). It appears that sexual selection imposed a reproductive cost on the control populations that outweighed any adaptive improvements that might have resulted from, for example, female choice. Holland and Rice are at pains to point out that sexual selection does not necessarily have a net detrimental outcome, only that it can.

What about good genes?

At first glance, this result contradicts the once-again fashionable position that mate choice is eugenic[9]. In particular, the results contrast with the findings of a similar experiment published in the same journal late last year[10]. Promislow, Smith and Pearse put five *D. melanogaster* males with each female in three replicate 'sexual selection' lines and three monogamous lines. There were few consistent differences in morphology after ten generations of the monogamy and sexual selection treatments, but the effects on age-specific mortality were palpable. In most cases, individuals from the sexual-selection lines lived longer than individuals from monogamous lines. The lower overall mortality in sexual-selection lines supports the notion that sexual selection leads to increased adult viability, possibly as a result of female choice for males with 'good genes'.

The apparent contradiction might be due to a simple difference between studies in the length of time that courtship and mating could occur. Promislow's team allowed males and females to interact for only three hours. This is sufficient time for males to fight for first access to females, and females to exercise precopulatory choice. According to their own observations however, it is not long enough for multiple mating to occur. In Holland and Rice's experiment, males and females interacted for five days, allowing ample time for multiple mating, with consequent sperm competition and cryptic female choice. It would appear, therefore, that the costs of sexual selection can be laid at the door of postcopulatory processes. In *Drosophila* this makes sense, because the frequency of remating[1] and sperm toxicity[7] are both known to reduce female longevity.

Holland and Rice's study also conflicts with several recent studies where multiple mating increased offspring viability, with no apparent cost to fecundity[11]. Interestingly, the common explanation in these studies is that cryptic female choice reduces genetic incompatibility. If true, we would not necessarily predict that polyandry will cause a long-term increase in a population's reproductive output, because female choice for compatibility is idiosyncratic rather than for universally better 'viability genes'. Experimental approaches that manipulate the opportunity for pre- and postcopulatory sexual selection[8,10] might reveal not only whether genetic incompatibility favours a tendency for females to mate multiply, but also whether polyandry allows the continuing segregation of incompatible alleles in a population.

Resistance is inevitable

The net effect of sexual selection on a population's reproductive output depends on the relative costs and benefits. Postcopulatory costs resulting from sperm competition have been well publicized. Even so, precopulatory ones should not be ignored. The risk of injury during coercive mating attempts[3] and energetic and predation[2] costs to courted or guarded females are known to be important. Moreover, male exploitation of existing female

sensory preferences might result in females mating suboptimally[6,12]. Female resistance to these costs should be selected for in just the same way as resistance to adaptations for male sperm competition[6]. We need to calculate the relative magnitude of the costs of these different sexually selected processes (as well as the size of the benefits accrued). No doubt Holland and Rice's study will spawn more refined investigations of the population-level effects of various sexually selective processes under a diversity of conditions. These might reveal whether sexual selection has long-term effects that are, on average, advantageous or costly at levels above the individual.

Holland and Rice[6] have previously suggested that resistance by females to male display, coercion, and harmful male competitive adaptations can influence the outcome of male competition, resulting in a process they dubbed chase-away sexual selection. Resistance might take the form of females requiring greater stimulation to mate, or chemical defences against seminal-fluid components that bias the outcome of sperm competition[8]. In each case, it might drive further exaggeration of male display or seminal selfishness.

Chase-away was proposed[6] as a general mechanism of sexual selection emerging from intersexual conflict. In 1972, Trivers[5] showed us that conflict of interest between the sexes can shape whether and how sexual selection operates in populations. It has taken nearly 30 years to show that the reverse is also true: that the intensity of sexual selection determines the intensity of sexual conflict and shapes the evolution of further adaptations to ameliorate its consequences. The generality of the chase-away model, and its explanatory power compared with other models of preference evolution have already stimulated lively debate[12–14]. The evolutionary importance of female resistance to male competitive adaptation could provide a fruitful new direction to the study of sexual selection.

Robert Brooks

School of Tropical Biology, James Cook University, Townsville, 4811, Australia (rob.brooks@jcu.edu.au)

Michael D. Jennions

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama (jennionm@naos.si.edu)

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