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Research Focus

Sex, death and tragedy

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The population consequences of sexual conflict are relatively unexplored. In a recent paper, Le Galliard *et al.* now show that males of the common lizard *Lacerta vivipara* cause such damage to females that male-biased populations decrease in size, posing a real risk to the persistence of local lizard populations. Their study reveals surprising parallels between sexual conflict and the tragedy of the commons, where selfish competition over females destroys the very resource (i.e. the females) over which the males are fighting.

Introduction

The battle over access to mates is perhaps one of the most extreme conflicts in evolution. Male–male conflict sometimes becomes so intense that it can result in the death of all males in the population. For example, in marsupials of the genera *Antechinus* and *Dasyurus*, the diseases that appear to follow from excessive investment in mating can wipe out all males in the population after the mating season [1,2]. This is not harmful to population persistence, however, as inseminated females produce new males. If males can invest so much in sex that they eventually kill themselves, to what extent will they harm a potential mate?

The answer is that males often harm females [3]. For example, in feral sheep, male harassment is associated with an increase in female mortality [4], and in red-sided garter snakes *Thamnophis sirtalis parietalis*, too-eager males suffocate females, causing significant female mortality [5]. But could the damaging effect on females become as severe as the unavoidable death of males in marsupials (which would obviously be bad news for population persistence)?

Sex and death

It is impossible to observe reproductive strategies that do not enable populations to persist. However, experimental manipulations can tell us just how close populations are to the danger zone. In a new study [6], Le Galliard and colleagues created enclosures of male-biased (78% males) and female-biased (22% males) populations of common lizards *Lacerta vivipara*. The authors quantified different aspects of harm influenced by males on females. Female-biased populations showed relatively little evidence of male harm, and males and females had similar survival probabilities. However, in male-biased populations, the situation appeared dire for the female lizards, with a drop in survival, fecundity and emigration probability. Females showed two to three times more scars and wounds in male-biased populations compared with females in female-biased populations, and there are several previous studies that detail how male harassment inflicts costs on females through biting [7], stress [8] and loss of energy [9]. While males harassed females to a greater extent when faced with extra competition, there did not appear to be any noticeable evidence for male–male competition inflicting costs on the males themselves; neither did males attempt to emigrate from male-biased populations to any greater extent than they did from female-biased ones.

The adult sex ratio consequently had a much larger effect on population growth than one would predict based on the fact that only females give birth. Whereas female-biased populations grew by ~50%, male-biased populations were reduced by a half after breeding. To estimate how such a result would affect population persistence, the authors built a stage-structured model with stochastic sex-ratio fluctuations, which revealed that the extinction risk owing to such stochasticity increased as a result of male aggression: incorporating male aggression in a model of an isolated population led to probable extinction within 40 years.

Natural populations of the common lizard are female biased owing to high male mortality, and the study by Le Galliard *et al*. [6] points out how this, in itself, could be necessary for preventing population collapse. The implications of the research should influence both population ecology, by demonstrating that ecologists should start to realize that males can have a greater influence on demography than was previously thought, and behavioral ecology, being the first study to show clearly that sexual conflict can have disastrous effects at the population level.

Do males matter?

Population ecology has long assumed that males have little role in population dynamics, and many ecologists have simplified their models by removing males from the picture. Le Galliard *et al.* [6] have done an excellent job of pointing out how poor such approximations can be. Males (or rather the lack of males) have previously been linked to a population decline in the Saiga antelope *Saiga tatarica* [10], and such effects might be general [11]. However, few studies have documented how an excess of males can affect population density, despite such ideas being present in the behavioral ecology literature [11–15]. If female survival is adversely affected by a male bias in the adult sex ratio, the result can be a vicious circle of increasing male bias

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and a further reduction in female survival prospects. This suggests that the sex ratio should be an important factor in conservation biology. Having a better understanding of how a population will respond to changes in the adult sex ratio, such as sex-specific culling or climatic effects on sex determination, could prove essential in conserving a species.

Sexual conflict and the tragedy of the commons

For males, females are a resource required for reproduction. Sharing a limited resource is never easy, particularly when the resource is prone to disappear. An aspect of sexual conflict that has so far received little attention is that the cost of an action is borne by someone other than the actor; if an individual male procures a benefit, females might pay most of the cost. Hardin [16] described the 'tragedy of the commons' as a case in which individuals gain benefits but at a cost of diminishing the total resource; in the absence of advanced policing or negotiation mechanisms, the prediction is that the resource will be continually reduced until it disappears entirely [16]. Whereas researchers of social evolution have long realized the tragedy of the commons as a consequence of conflict in their systems [17,18], the sexual selection and sexual conflict literature seems somewhat oblivious to these ideas. The results of Le Galliard and colleagues [6] seem to fit the tragedy framework well. Such a result begs the question of how sexual conflict can exist [19] and why populations are not repeatedly driven to extinction as a result.

Perhaps the most obvious way that extinction could be prevented in the common lizard system is through female resistance to male harassment. This does not seem to be the case, however, as one of the less obvious results of the study [6] is that females emigrated more from female-biased, than from male-biased, populations. This suggests that, although females have the ability to minimize female–female competition, they do not do the same to minimize male harassment. The authors point out that rapidly declining populations lack the potential to evolve, which might be a reason for the lack of female resistance.

As the authors only documented population decline over one generation, they might not have seen the full picture, and we do not know if artificially created male-biased populations would eventually go extinct, or if some other process would stabilize the population. For example, it has been suggested that at lower population densities it is less advantageous for males to harm females owing to the density-dependent benefits of harassment [19]. An example of these benefits could be greater encounters at high density, which would increase the relative benefit gained from harassing females [19]. Alternatively, Le Galliard *et al*. [6] point out that sex-biased mortality does vary over space and time, suggesting that existing lizard populations are simply the lucky ones in which mortality patterns have created a female-biased population.

Conclusion

The study discussed here represents an important contribution to linking population and behavioral ecology. The authors make clear that males do make a difference to population processes. Behavioral ecologists repeatedly talk about costs, but until recently there has been little discussion of how these costs can feedback to influence population growth and persistence. There are more examples of sexual conflict in the literature that should have an influence on population ecology and persistence. Le Galliard *et al*. [6] have detailed an important contribution to what might potentially prove to be a much larger problem in the study of populations and their behavior.

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