Can punishment maintain sex?

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Individuals who reproduce asexually have a two-fold advantage over their sexually-reproducing counterparts as they are able to reproduce twice as fast. Explaining why sexual reproduction is favoured over asexual reproduction therefore remains an important challenge in evolutionary biology. Various mechanisms involving resistance to parasites, adaptation to novel environments and helping to purge the genome of deleterious mutations have all been proposed as potential mechanisms which could promote the evolution of sex. A recent article has suggested that spiteful males may help to reduce the two-fold advantage of asexual females. Here I discuss this idea, and further ask whether punishment of asexual females by sexual females could be one way in which sexual reproduction could be maintained in groups of animals; in light of recent research on the repression of competition, it could be possible that asexual females which reproduce faster than their sexual counterparts will be punished for using group resources. It may therefore be possible that the behaviour of sexual individuals towards asexual females could have fitness consequences which could potentially reduce the two-fold advantage they gain from reproducing parthenogenetically.

The maintenance of sex

Explaining the evolution of sex remains one of the great challenges in evolutionary biology (Maynard Smith 1978). Sexual reproduction represents a paradox, because any allele which reproduces asexually will have a two-fold advantage over an allele which reproduces sexually. This is known as the "two-fold cost" of sex (Maynard Smith 1978), and represents a demographic cost where asexual individuals avoid producing costly males, and therefore may produce twice as many females.

Parthenogenesis is widespread in many taxa (Olsen 1975, Groot et al. 2003, Chapman et al. 2007). Despite the fact that, in many species, sexual females are able to reproduce parthenogenically, and the large demographic cost of reproducing sexually, sexual reproduction is highly common in nature (Maynard Smith 1978). Various arguments have been put forward to explain the maintenance of sex. One of the most widely invoked explanations for why a sexually-reproducing population is immune to invasion from asexuals is that sex can help a host to change genotypes each generation and to evade parasites that way (Hamilton et al. 1990, Agrawal 2006). Sex can also help to purge genomes of deleterious mutations (Kondrashov 1988) and can promote adaptations to new environments (Fisher 1930, Felsenstein 1974). These factors all favour sexual reproduction over asexual reproduction, as they help to reduce the two-fold cost of producing males.

Can spiteful male harassment punish asexual females?

Male behaviour can have both negative and positive effects on female fitness (Rankin and Kokko 2007). A large proportion of male behaviours, such as male harassment of females, can affect female fitness in a negative way (Arnqvist and Rowe 2005), and as such will be likely to add to the two-fold cost of sex (Rankin and Kokko 2007). Despite the costs and benefits that male and female behaviours may have on female reproduction, individual-level behaviour has rarely been invoked as a potential mechanism to maintain sexual reproduction.

However, a recent paper (Dagg 2006) has suggested that spite, in the form of male harassment of asexual females, could help to outweigh the two-fold cost of sex, and maintain sexual reproduction. Dagg (2006) suggests that, when a sexually-reproducing lineage splits to produce both sexually reproducing and asexually reproducing females, male harassment of asexual females may act to punish the asexual females. Such behaviour would be seen as a spiteful relationship, because males which harm asexual females pay a cost (in terms of lost reproduction due to mating with asexuals), and also inflict a cost on the asexual females (by harassment).

Spiteful behaviours are behaviours which are costly to both the actor and the recipient (Gardner and West 2004a,b). Despite having a direct cost, such behaviours can evolve if the allele for spiteful behaviour has a lower

chance of occurring at the same locus in the individual receiving the spiteful behaviour (Gardner and West 2004b). In other words, relatedness, r, is less than zero. The benefit to the actor comes from improving her inclusive fitness: by harming a less-related individual at a cost to herself, she indirectly makes life easier by reducing competition for more related individuals. In other words, spiteful behaviour can be altruistic, and can be explained by Hamilton's rule (Hamilton 1964), which tells us that spiteful behaviour will be able to evolve if rb-c > 0.

Dagg's (2006) argument is that if a mutation arises at a particular locus in a male, which causes the male to harm an asexual female at a cost to himself, then this allele will be able to spread through males in the population as it has a negative relatedness (r = −1) to an allele at the same locus in the asexual female (Dagg 2006). This means that the cost to the male of such spiteful behaviour, in terms of lost matings or actively engaging in conflict with an asexual female, will be outweighed by the benefit the spiteful behaviour has on the males relatives, and hence the spiteful behaviour will evolve.

At first glance, this argument makes sense, because it is clear that an allele in a male will have a relatedness of −1 to an allele at the same locus in an asexual female. However, to truly understand how a spiteful mutation will arise, we need to think about all parties in the population. Spite is effectively an altruistic act, where the acting individual suffers a cost, while benefiting its relatives by eliminating less related competitors. If a male can differentiate between sexual and asexual females, he will have a higher fitness if he preferentially mates with sexual females. Any male who differentiates between sexually-reproducing and asexually reproducing females, and chooses to spend time harming asexual females (rather than searching for mates), will loose matings to his competitors. As a result, all males (and sexual females) will benefit from freeing up resources wasted by asexual females, and thus the spiteful male will not only be helping his relatives, but also his competitors. This means he will have a lower fitness than other males in the population. Thus, the act of males preferentially harassing females should not be seen as spiteful, but rather as an act of altruism towards other males in the population. However, there is a problem with this argument: it is important to realise that here it is of no relevance that an allele in a male has a relatedness of −1 to an allele in an asexual female. A male spitefully harming an asexual female would be akin to an individual of one species paying a cost to harm an individual in another species. Such an individual will pay a cost to itself, while conferring benefits on it's conspecific competitors (Foster and Wenseleers 2006). What matters most strongly is the feedback, in the form of an indirect benefit, that the acting individual gains from the costly behaviour (Lehmann and Keller 2006).

In most circumstances, males will face stronger competition for matings than they would for resources that might be shared with asexual females. Of course, if males were competing over resources such as territories or food, then they may get a direct benefit from chasing away asexual females. In such a case, the behaviour would not be regarded as spiteful, but selfish (West et al. 2007), as there would be a direct cost to the asexual female (the "recipient") but a direct benefit to the male (the "actor").

Female resistance to male harm will come at a cost to females. A mutant female that reproduces asexually would still be pursued by males, as it is likely that males would not be able to discriminate between asexual and sexual females. Females have been shown to lose their resistance to male harm in a few generations if they are not exposed to males (Rice 1996, Wigby and Chapman 2004). A chance separation from the harmful effect of males, for just a few generations, may be enough for asexual females to lose resistance, making them prone to the costs of male harassment should they encounter a male in later generations (Dagg 2006). Of course, if males are both harmful to females and continually fail to discriminate against asexuals, then there will be a strong selective pressure for asexuals to maintain resistance to the effects of male harm.

Females punishing females

If it is unlikely that male behaviour towards asexual females can maintain sex, is it possible that the behaviour of sexual females could reduce the two-fold benefit gained by asexual females? The behaviour of sexual females will be more likely to have a stronger influence in reducing the two-fold cost of sex. Asexually-reproducing females have a higher growth rate, and as such will destroy any common resource much faster than females which reproduce sexually (Nunney 1989, 1999). As a result of this, asexual reproduction can easily lead to an evolutionary tragedy of the commons (Hardin 1968, Rankin et al. in press), as asexual females gain a selfish advantage whilst over-exploiting the common resource used by both asexual and sexually-reproducing individuals.

One of the most commonly invoked ways to resolve the tragedy of the commons is through coercion (Ostrom 1999, Frank 2003), where other members of a group repress the selfish actions of other individuals. Punishment, where individuals stepping out of the social norm suffer costs inflicted by other members, can evolve and promote group-beneficial behaviours (Clutton-Brock and Parker 1995, Frank 2003). Punishment and policing behaviour can be seen across a wide range of taxa, and can potentially apply to microorganisms as much as higher vertebrates (Frank 2003, West et al. 2006). Policing has been shown to repress competition in social insect colonies, where workers police the eggs of other workers, ensuring that only the queen contributes to reproduction, and the colony stays intact (Ratnieks et al. 2006, Wenseleers and Ratnieks 2006).

Can punishment ever evolve to repress asexual reproduction? As females who reproduce asexually have a higher growth rate, they are more likely to destroy group resources. Under strong group structure, there will be a high incentive for other members of the group to repress such reproduction, and to keep overall group productivity to a level where group resources are not over exploited (Frank 1995). Some group structure is needed for punishing behaviour to occur under such a scenario (Frank 1995, 1998, 2003). In the absence of any group structure, each individual would do best to produce as many offspring as they possibly could, and hence asexual females, with their two-fold growth rate, would prevail. However, with high within-group relatedness (where asexual females would be more related to other,

sexual, members of their group than to the rest of the population) simple self-restraint is favoured and group competition is reduced (Frank 2003). Under lower relatedness, which would normally not favour self-restraint, policing of other group members can be advantageous (Frank 2003). This can help to unite both individual and group interests, and favour prudent behaviours.

Dagg (2006) suggested that the production of sons could be a strategy by sexual females to punish asexual females. This fits into the idea of punishment, where the sexual females pay a clear fitness cost but gain a benefit by harming their asexual competitors (to whom they are less related). For such a system to occur, linkage disequilibrium between sex-ratio distorting genes and those controlling for sexual reproduction would be required. Such a strategy would only work under high levels of male harm towards females, as in the absence of male harassment, producing extra males would have little effect on the fitness of asexual females.

In principle, punishment of asexually reproducing females could work whether or not punishing females are able to differentiate between sexually- and asexually-reproducing individuals: all that would be needed would be to recognise which individuals produce more offspring than the group "norm", and to police accordingly. As such, punishment of asexuals could be a simple by-product of reducing other forms of reproductive selfishness. Of course, it may be difficult to recognise the offspring of an asexual female, and the first generation will not affect group resource levels, as males are simply replaced by females. However, a simple strategy of killing excess females in a group would be enough to keep potential asexual lineages at bay. As such, punishment will be more likely to have an influence on the maintenance of sexual reproduction if prior control mechanisms already exist. For example, if females already actively control their sex ratio and police excess females, then any female reproducing asexually will suffer a cost. By repressing competition, group members can reproduce at a level that is optimal for the group, thus aligning the interests of the individual with the interests of the group (Frank 2003).

Conclusion

Whilst male spite towards asexual females (Dagg 2006) is unlikely to be a factor involved in the maintenance of sex, punishment and policing by sexual females could potentially maintain sexual reproduction. This will occur when it is to the advantage of sexual females to repress competition caused by asexually-reproducing females. How common this is remains to be seen, and it may depend strongly on cognition: it is important for the punishing individual to recognise that a given female is asexual, and to punish accordingly. However, if there is already a system under which excess production of females is punished, then asexual females will automatically be punished. This, in itself, may be enough to outweigh the cost of sex and prevent asexual lineages from invading. It is well known that sex can reduce the incidence of deleterious mutations (Kondrashov 1988) or increase resistance to parasites (Hamilton et al. 1990, Agrawal 2006). As discussed above, it could be possible that the fitness consequences of individual-behaviours, such as punishment of asexual females, may play a role in reducing the two-fold cost of sex, and maintaining sexual reproduction.

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