Opinion

Sexual Conflict, Facultative Asexuality, and the True Paradox of Sex

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Theory suggests that occasional or conditional sex involving facultative switching between sexual and asexual reproduction is the optimal reproductive strategy. Therefore, the true 'paradox of sex' is the prevalence of obligate sex. This points to the existence of powerful, general impediments to the invasion of obligately sexual populations by facultative mutants, and recent studies raise the intriguing possibility that a key impediment could be sexual conflict. Using Bateman gradients we show that facultative asexuality can amplify sexual conflict over mating, generating strong selection for both female resistance and male coercion. We hypothesize that invasions are most likely to succeed when mutants have negative Bateman gradients, can avoid mating, and achieve high fecundity through asexual reproduction – a combination unlikely to occur in natural populations.

Obligate Sex Is the Real Paradox

Why sexual reproduction is so widespread despite its substantial costs is one of the most important unsolved problems in evolutionary biology. Because sex is associated with numerous short-term costs that asexual organisms mostly avoid (e.g., [1–9]), theory predicts that asexual or parthenogenetic lineages should outcompete and outnumber sexual lineages, all else being equal [3]. However, paradoxically, sex is the dominant mode of reproduction in many lineages of complex eukaryotes [10].

Evolutionary biologists have long tried to resolve this paradox by searching for countervailing benefits of sex while generally treating sexual and asexual (parthenogenetic) reproduction as mutually exclusive strategies occurring in separate individuals or populations [3,6]. However, a large body of theory suggests that facultative reproductive strategies (where individuals can switch between sexual and asexual reproductive modes) should be more successful than obligate strategies because occasional sex provides all the advantages of obligate sex but with fewer costs [11–13] (although see [14]). For example, rare or occasional sex prevents the accumulation of deleterious allele combinations [15], promotes the fixation of beneficial mutations [11,16], facilitates adaptation [17], and enhances evolvability [18] as efficiently as obligate sex does. Furthermore, models suggest that sex is beneficial only under certain conditions; for example, in low-quality individuals [19,20], in populations affected by highly virulent parasites [21], or in environments undergoing rapid change [22]. The ability to switch between sexual and asexual reproductive modes to match prevailing conditions should therefore, in principle, be highly advantageous and should outperform both obligate sexual and obligate asexual strategies. However, while facultative reproductive strategies are the norm in unicellular eukaryotes [23], many multicellular eukaryotes – including the vast majority of animals – are obligately sexual [10]. Thus, the crux of the paradox is not why sex is common in metazoans, but why

Trends

The rarity of facultative asexuality in animals is the true paradox of sex.

Factors that impede facultative mutant invasions could be key to this paradox.

Bateman gradients can affect the invasive potential of facultative mutants.

Obligate sex might persist because sexual conflict limits mutants' fitness.

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facultative reproductive strategies are so rare. More specifically, since obligate sexual reproduction appears to be ancestral in many lineages of multicellular eukaryotes [24], the most salient question is why facultative reproductive strategies are rarely able to invade obligately sexual populations.

The prevalence of obligate sex indicates the existence of powerful, taxonomically widespread factors that inhibit the evolution of reproductive plasticity in many metazoan lineages by preventing facultative mutants from successfully invading obligately sexual populations. Several recent studies have raised the intriguing possibility that a key factor could be sexual conflict, but the role of sexual conflict in promoting and maintaining obligate sexuality remains poorly understood. Here we use Bateman gradients to show that the possibility of reproduction without mating can exacerbate sexual conflict over mating frequency in facultatively asexual (parthenogenetic) systems, which can in turn affect the dynamics of sexually antagonistic coevolution. We argue that these effects could be key to understanding the ability of obligately sexual populations to resist invasion by facultative mutants.

Sexual Conflict: A Neglected Factor in Facultative Systems

Sexual conflict is a universal phenomenon in sexually reproducing organisms, occurring whenever traits shared by males and females (e.g., mating rate) have sex-specific fitness optima that cannot be attained simultaneously (e.g., low mating-rate optima for females versus high mating-rate optima for males [25,26]). Sexually antagonistic selection can drive the evolution of traits that maximize the fitness of one sex while imposing costs on the other sex [27,28], potentially resulting in a coevolutionary 'arms race' between the sexes [25,26,29]. Sexual conflict and sexually antagonistic coevolution represent significant additional costs of sex [30,31] that deepen the paradox of sexual reproduction [1]. However, sexual conflict has yet to be fully incorporated into theories on the evolution and maintenance of sex (although see [32–38]).

Recent studies suggest that sexually antagonistic selection that drives the evolution of male coercion could be a direct mechanism by which parthenogenetic strategies in metazoans are inhibited (Box 1). Most of these studies focus on the consequences of sexual conflict for the incidence of sexual and asexual reproduction within facultative systems. How sexual conflict might influence the likelihood of facultative parthenogenesis evolving from an obligately sexual ancestral state remains largely unexplored.

We address this gap by using Bateman gradients, which are functions that relate fitness to mating rate [39], to illustrate how sexual conflict over mating could constrain the evolution of facultative parthenogenesis. Bateman gradients are a classic tool for representing sex differences in fitness variance and for identifying which sex experiences stronger sexual selection [40]. However, they can also be used to visualize the degree to which evolutionary interests differ between the sexes [25,41] and can therefore reveal how sexual conflict over mating frequency differs between obligately sexual and facultatively parthenogenetic populations and how these differences might determine the invasive potential of a facultative reproductive strategy. Although many traits can be subject to sexual conflict [26], we focus specifically on mating frequency since reproductive mode in many facultatively parthenogenetic animal systems is conditional on whether mating occurs [42,43]. This makes mating frequency the trait most directly relevant to understanding the probability of facultative invasions under scenarios of sexual conflict.

Consider a population reproducing via obligate sex (Figure 1A). The y-intercepts of male and female Bateman gradients (representing the fitness attained by each sex as virgins) are always 0 because no offspring can be produced without mating. Since both sexes can gain fitness only after their first mating, gradients are always positive at the origin (Figure 1A). However, the sexes

Box 1. Sexually Antagonistic Coevolution in Facultatively Asexual Systems

Sexual conflict can influence the incidence of sex and parthenogenesis in facultatively asexual systems where mating induces a switch from parthenogenetic to sexual reproduction. Coercion can promote sexual reproduction when males (re)enter the mating pool more quickly than females [33] and when population density is high [37]. Facultatively asexual populations can transition to obligate parthenogenesis when females effectively resist male coercion, either by acquiring resistance mutations [33] or by resisting in low densities when payoffs to resistance are greatest [37]. These dynamics set the scene for sexually antagonistic coevolution.

Sexual conflict over mating frequency has the potential to drive sexually antagonistic coevolution in facultatively parthenogenetic systems. If females are selected to avoid all matings (i.e., Bateman gradients are negative) and if sufficient genetic variation for resistance is available, linkage disequilibrium can be established between parthenogenesis and high resistance. This could potentially lead to the loss of sex through the extinction of males [38]. However, female resistance will select for more effective coercion by males [26] and the evolution of more coercive strategies could inhibit asexual reproduction. Asexuality might therefore be most likely to invade and spread when females can maintain the upper hand in sexually antagonistic coevolution. Consistent with this prediction, selection appears to have driven the rapid loss of mate-attracting pheromones, as well as mating and fertilization ability, in several asexual lineages of *Timema*s tick insects [47]. These losses could represent adaptations for effective resistance and may have played a role in transitions to obligate asexuality in these species.

Effective resistance might facilitate the invasion of obligately sexual populations by facultatively asexual mutants. However, even when facultative parthenogenesis and effective resistance co-occur, resistance and reproduction could trade off such that the costs of resistance negate the benefits of asexual reproduction. Such a tradeoff could result in reduced reproductive output in females that manage to avoid mating and reproduce asexually, further entrenching sexual reproduction. The potential for facultatively asexual mutants to invade obligately sexual populations could therefore depend not only on the relative shape and slope of mutants' Bateman gradients but on standing genetic variation in female resistance and male coercion, on the costs of resistance, and on the dynamics of sexually antagonistic coevolution. Facultative reproductive strategies might be so rare in animals because the complex preconditions for such invasions are very seldom realized.
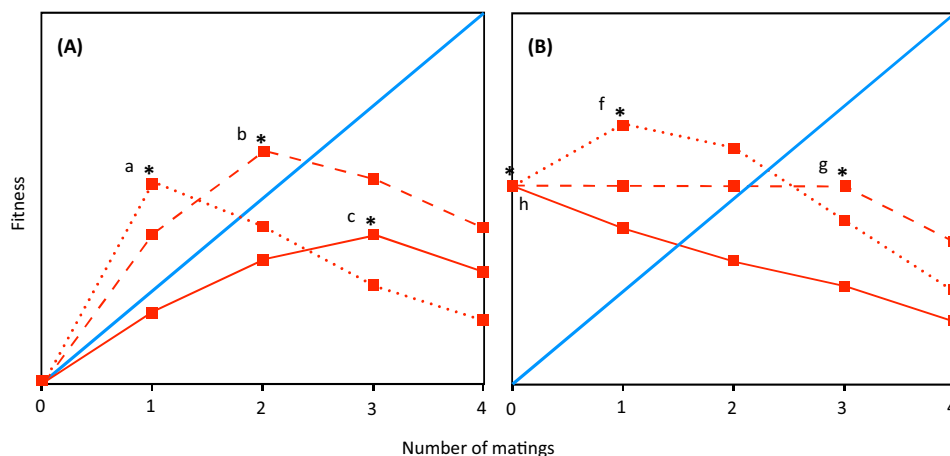
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Figure 1. Bateman Gradients for Hypothetical Populations of Obligately Sexual (A) and Facultatively Parthenogenetic (B) Organisms. The male Bateman gradient (in blue) is assumed to be positive and linear in both populations. Differences in slope and shape between female fitness functions (in red) reflect variation in the benefits and costs of each additional mating for female individuals within each population. Note that facultatively parthenogenetic females [(B) in red] reproduce asexually when the number of matings is 0 but sexually with matings ≥1. The hypothetical optimal number of matings for each female is indicated by an asterisk on each curve. Sexual conflict over mating frequency occurs in both populations when female mating frequency exceeds this optimum, causing gradients to become negative. In an obligately sexual population, females are never selected to avoid their first mating [gradients a, b, and c in (A)], whereas in a facultatively parthenogenetic population females can be selected to avoid all matings [gradient h in (B)]. The shape of these fitness functions could therefore determine the likelihood of facultative parthenogenesis invading sexual populations. Invasions will be most likely when facultative mutants possess negative Bateman gradients [h in (B)] because alleles for parthenogenesis should spread more frequently when mutants are selected to avoid all matings.

often differ in the steepness and shape of their gradients beyond the first mating. In most species male gradients are assumed to be positive and linear because each additional mating confers fitness benefits to males. However, female gradients are expected to become negative after a certain number of matings per reproductive cycle or lifetime because excess copulations tend to impose fitness costs without compensating benefits (Figure 1A). In many species females can receive sufficient sperm from a single mating to fertilize all of their eggs, and additional matings could expose females to harmful seminal fluid proteins [44], mechanical damage [45], or predation risk [46] without increasing their fecundity. This misalignment of the sexes' optimal mating frequencies generates sexual conflict: beyond a certain number of matings, males benefit from additional matings while females only pay a cost [25]. In such species, when a male encounters a female, he will typically benefit by trying to mate but she will often benefit by trying to avoid mating. Importantly, however, resistance to mating will be favored by selection only in females that reach their optimal mating frequency. Virgin females will seek to mate, although they might be selected to exercise mate choice and reject low-quality males.

Now consider a facultatively parthenogenetic population where females have the capacity to either reproduce asexually as virgins or to mate and switch to sexual reproduction (Figure 1B), a reproductive strategy characteristic of many phasmatids [47] and ephemeropterids [48]. The y-intercept of the Bateman gradient (and therefore fitness as a virgin) is still 0 for males but is >0 for virgin females (Figure 1B). From this non-zero starting point, the female gradient can in principle be initially positive, flat, or negative (Figure 1B, gradients f, g, and h, respectively). Females with an initially positive gradient gain fitness with each additional mating until an optimum is reached, at which point mating interests between the sexes diverge, leading to sexual conflict (Figure 1B, gradient f). Females with an initially flat gradient neither gain nor lose fitness with additional matings and experience no sexual conflict over mating frequency unless mating eventually becomes costly (Figure 1B, gradient g). By contrast, females with an initially negative gradient lose fitness with every mating and therefore experience conflict over mating even as virgins (Figure 1B, gradient h). Such females will be selected to resist all mating attempts.

Can Sexual Conflict Help to Resolve the Paradox of Obligate Sex?

The Bateman gradients in Figure 1 show why sexual conflict can be more intense in facultative systems than in obligately sexual systems: facultative females can be selected to avoid all matings whereas obligately sexual females cannot. Because facultative mutants with negative Bateman gradients will be under selection to resist all mating attempts, such mutants will be more likely to reproduce asexually and, all else being equal, will be more likely to invade an obligately sexual population than a mutant whose reproductive success is increased by mating (gradient h versus gradient f in Figure 1B). Since parthenogens inherit 100% of maternal genes while sexual offspring inherit only 50% of maternal genes, alleles for facultative parthenogenesis will spread faster when reproduction is mostly asexual.

However, the probability of a mutant simultaneously acquiring effective resistance and a capacity for facultative parthenogenesis is likely to be extremely low. Facultative mutants are expected to share the same levels of resistance as their sexual conspecifics. The ability of facultative parthenogenesis to spread through a sexual population will therefore hinge on whether linkage disequilibrium can build up between rare alleles for high resistance and facultative parthenogenesis, unless encounters between the sexes are sufficiently infrequent that mating can be avoided without resistance (see [38]). If either allele occurs at a very low frequency when mates are abundant, facultative strategies will rarely spread (Box 1).

The slope of the Bateman gradient for a facultative mutant is likely to be determined by a range of factors. One such factor could be the type of parthenogenesis expressed by mutants. Parthenogenesis occurs via several different mechanisms that vary in the level of heterozygosity

produced in offspring [49,50]. Apomictic parthenogenesis occurs without meiosis and results in offspring that are genetically identical to their mother [43,51]. By contrast, automixis by gamete duplication involves both meiosis and recombination with diploidy restored via post-meiotic doubling of the egg's chromosomes, resulting in parthenogens that are entirely homozygous [52]. The tendency for such homozygotes to express deleterious recessive mutations might reduce the fitness prospects of automictic mutants, at least initially (i.e., before the purging of deleterious alleles by selection). Such mutants might therefore benefit by mixing their genes with those of males to create heterozygous offspring and might be less strongly selected to resist mating than highly heterozygous apomictic mutants for whom sex has little effect on offspring heterozygosity. Negative Bateman gradients might therefore be more likely to occur in apomictic than in automictic mutants.

Other developmental or evolutionary constraints could also affect the slopes of facultative mutants' Bateman gradients and several hypotheses have already linked such constraints to the maintenance of sex [51,53–55]. Genetic and cytological constraints, such as limited diploidy restoration, failed activation of unfertilized eggs, and genomic imprinting, have been suggested to limit parthenogenetic development and reduce parthenogenetic fecundity and viability [51]. Such constraints are hypothesized to prevent the invasion of asexuality in taxa with longstanding obligate sex and anisogamy [53]. Bateman gradients clarify the role of such constraints in inhibiting facultative invasions. In the face of strong constraints on parthenogenetic fecundity and/or the viability of asexually produced offspring, facultative mutants might regularly express positive Bateman gradients, making invasions unlikely.

The shapes of Bateman gradients in facultatively asexual mutants, as well as their levels of resistance to mating, are poorly known. Differences in mating costs and fecundity between sexually and asexually reproducing females in facultative systems also remain relatively unexamined. However, a study on the facultatively parthenogenetic phasmatid *Extatosoma tiaratum* showed that females switching from parthenogenetic to sexual reproduction suffer increased mortality and reduced egg output compared with females reproducing only sexually or asexually [36]. Although this study did not quantify Bateman gradients, its findings suggest that the costliness of mating in a facultative system can depend on a female's prior mode of reproduction. This study also showed that females behaviorally resist mating attempts and produce male-repellant secretions [36], suggesting that costs of switching could have selected for mating avoidance. The costs of reproductive switching could be an additional factor limiting the potential for invasion by facultative mutants [36]. It would be interesting to know whether such costs occur in other facultative systems.

Bateman gradients could also inform research on the role of sexual conflict in the evolution of simultaneous hermaphroditism, given that selfing and outcrossing in simultaneous hermaphrodites is in many ways analogous to parthenogenetic and sexual reproduction in facultative parthenogens with separate sexes. Likewise, although Bateman gradients do not apply to non-mating animals such as broadcast spawners, the same logic could be extended to consider the role of sexual conflict over fertilization in such systems. In non-copulating animals sexual conflict is often mediated chemically [56], but the availability of genetic variation for both asexual reproduction (i.e., capacity for unfertilized eggs to develop) and resistance to fertilization could be similarly important as preconditions for successful invasions by facultative strategies.

Concluding Remarks
Theory suggests that a facultative reproductive strategy that occasionally utilizes sex can provide all the benefits of obligate sex with far fewer costs. Therefore, a key question for theoretical and empirical research is how obligately sexual populations withstand invasions by facultative mutants. We argue that the potential for such invasions to exacerbate sexual conflict

Outstanding Questions
What factors prevent facultatively asexual mutants from invading and supplanting obligately sexual populations?

How important is sexual conflict in facultatively asexual organisms and what are its manifestations and consequences?

How does sexual conflict influence the potential for facultative mutants to invade obligately sexual populations?

What are the shapes of female Bateman gradients in facultatively asexual mutants and in established facultatively asexual populations?

How do the mechanism of asexual reproduction (parthenogenesis) and physiological constraints on asexuality influence the shape of female Bateman gradients in facultative asexuals?

Is obligate sex maintained by similar factors in internally versus externally fertilizing organisms, in monoecious versus dioecious organisms, and in animals versus plants?

over mating can have important implications for the potential of facultative parthenogenesis to invade and displace obligate sex, with negative Bateman gradients likely to promote, and positive gradients likely to impede, the spread of facultative parthenogenesis. The role of sexual conflict in facultative systems represents a promising new direction for research on the maintenance of sex (see Outstanding Questions).

Acknowledgments

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