

The Costs and Benefits of Occasional Sex: Theoretical Predictions and a Case Study

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Abstract

Theory predicts that occasional sexual reproduction in predominantly parthenogenetic organisms offers all the advantages of obligate sexuality without paying its full costs. However, empirical examples identifying and evaluating the costs and benefits of rare sex are scarce. After reviewing the theoretical perspective on rare sex, we present our findings of potential costs and benefits of occasional sex in polyploid, sperm-dependent parthenogens of the planarian flatworm *Schmidtea polychoa*. Despite costs associated with the production of less fertile tetraploids as sexual intermediates, the benefits of rare sex prevail in *S. polychoa* and may be sufficiently strong to prevent extinction of parthenogenetic populations. This offers an explanation for the dominance of parthenogenesis in *S. polychoa*. We discuss the enigmatic question why not all organisms show a mixed reproduction mode.

Key words: asexual, evolution of sex, parthenogenesis, polyploidy, rare sex

A Theoretical View on the Costs and Benefits of Occasional Sex

Most theories on the evolution of sex consider obligate asexual versus obligate sexual reproduction only (Hurst and Peck 1996). The presence of occasional sex in predominantly asexual organisms, such as facultative or cyclic parthenogenesis, has often been ignored (Som and Reyer 2007). To our knowledge, the first consideration of “rare sex” came in 1939 from Sewall Wright who claimed that the “the combination of prevailing uniparental reproduction with occasional crossbreeding gives results with the favourable properties of both systems . . .” (Wright 1939). However, formal analytical investigations of occasional sex started more than 30 years later in the mid-1970s. Since then numerous models have been developed, which implement varying degrees of sex.

The Benefits of Occasional Sex

Most models revealed an increasing benefit of sex with increasing sex rate. Muller's ratchet, for instance, claims that asexual populations accumulate mildly deleterious mutations through repeated stochastic losses of the least-loaded clonal lineage. In sexual populations these genotypes can be restored by genetic mixing. However, this does not require maximal outcrossing. Low recombination rates can already

halt Muller's ratchet and prevent genome deterioration (Bell 1988; Charlesworth et al. 1993; Som and Reyer 2007). The rate of accumulation of deleterious mutations is drastically decreased by rare sex and indistinguishable from obligate sex when recombination is occurring every fifth generation (Pamilo et al. 1987). After only one sexual generation most of the hidden genetic variance of asexuals is released and consequently the deleterious mutations can be efficiently eliminated by natural selection (Lynch and Gabriel 1983; Wagner and Gabriel 1990).

Similarly, most of the benefits described by the “deterministic mutation” hypothesis may also be obtained through rare sex, which has been shown to be sufficient to remove synergistically acting deleterious mutations (Kondrashov 1984; Hurst and Peck 1996). Assuming multiplicative effects of deleterious mutations on fitness, alternative reproduction modes such as automixis, which includes meiosis and syngamy, result in a drastically reduced mutational load compared with apomictic parthenogenesis (Haccou and Schneider 2004).

In comparison with obligate asex, rare sex is also beneficial in adapting to drastically changing environments (Maynard Smith 1971). Under certain conditions low recombination rates are evolutionarily stable in spatially and temporally fluctuating environments (Sasaki and Iwasa 1987). Under negative frequency-dependent selection, which

is the prerequisite for the Red Queen and parasite models, facultative sexuals are often able to invade populations with obligate sex or asex (Yamauchi 1999; Yamauchi and Kamite 2003). Specifically, for host–parasite models, occasional sex reduces the magnitude and complexity of population fluctuation. Moreover, low to intermediate frequencies of sex may even stabilize complex host–parasite dynamics to a greater extent than obligate sex (Flatt et al. 2001).

The Fisher–Muller hypothesis, which claims that sexual reproduction enhances the fixation probability of beneficial mutations, also applies to low levels of sex. The frequency of beneficial mutations is largely increased if asexual populations show low segregation rates (Hedrick and Whittam 1989; Green and Noakes 1995) or low recombination rates (Pamilo et al. 1987; Green and Noakes 1995). In addition to the classical Fisher–Muller models, rare sex may also accelerate the incorporation of extremely rare, beneficial mutations arising in populations that are prone to frequency-dependent selection (Peck 1993). Moreover, if a favorable mutation arises in a genome with deleterious mutations, sex rates of 5–10% largely increase the probability of its fixation (Peck 1994). Even if each deleterious mutation only slightly reduces fitness, but these suboptimal genes can rise to high frequencies due to genetic drift (drift load), the incorporation of beneficial mutations is enhanced by small amounts of sex (Peck et al. 1997). Hence, increasing rate of sex tends to increase mean fitness, whereas the largest increase in fitness occurs when the sex rate increases from small values (Peck 1994; Peck et al. 1997).

Low levels of sex leave clear population genetic signatures, which may resemble those of fully sexual populations (Halkett et al. 2005). For instance, rare sex leads to degrees of allelic variation indistinguishable from sexual populations (Bengtsson 2003). However, if sex is too rare intraindividual allelic divergence reaches magnitudes of purely asexual populations (Bengtsson 2003; Ceplitis 2003). This is important as high intraindividual allelic divergence is supposed to indicate long-term clonality (so-called Meselson effect). Moreover, rare sexual events increase the genotypic diversity (Balloux et al. 2003; Bengtsson 2003).

Even low sex rates create sufficient variation among offspring to improve the efficacy of natural selection and therefore increase mean fitness of a population (Burt 2000). The rates of phenotypic evolution may be even higher with periodic sex than with obligate sex as the periodic release of hidden genetic variance allows a population to rapidly adjust to new selective pressures (Lynch and Gabriel 1983).

In summary, a surprising high number of studies indicate that 5–10% of sex is sufficient to gain the advantages of 100% sex (e.g., Lynch and Gabriel 1983; Hedrick and Whittam 1989; Charlesworth et al. 1993; Green and Noakes 1995).

The Costs of Occasional Sex

There has been considerable debate on the intrinsic fitness cost an individual pays for occasional sex. Most models refer to cyclical parthenogenesis and differ in respect to whether

the cost of sex should be calculated per cycle or averaged per generation (Rispe and Pierre 1998). In the latter case, the costs of cyclical parthenogens increases by 2-fold as a purely asexual mutant can double its frequency compared with cyclical parthenogens with one complete generation of sex (Bulmer 1984; Rispe and Pierre 1998). Conversely, in the former case, the costs of sex are frequency dependent and strongly reduced in species with relatively few sexual generations (Charlesworth 1980, 1982). Thus, the view of a reduced cost of sex in facultative parthenogens is widely accepted (e.g., Lewis 1987; Green and Noakes 1995; Joshi and Moody 1995, 1998; Hurst and Peck 1996). Hence, species with rare sex theoretically gain the benefits of sexual reproduction without paying much of its costs.

However, relatively little effort has been made to empirically study the effect of rare sex on the persistence and success of parthenogenesis. In the following, we review our findings of occasional sex in predominantly parthenogenetic planarian flatworms to illustrate the cost and benefits in an empirical example.

An Empirical Example of the Costs and Benefits of Occasional Sex

The Study System *Schmidtea polychroa*

The freshwater planarian *S. polychroa* Ball (formerly named *Dugesia polychroa* Schmidt) is a flatworm of up to 25 mm in length and is widespread in most lakes and streams across Europe. In *S. polychroa* both sexual and parthenogenetic reproductive types are present. Sexuals and parthenogens are simultaneous hermaphrodites with internal fertilization but are incapable of self-fertilization. Reproductive types differ principally in ploidy level: sexuals are always diploid ($2x = 8$); parthenogens always polyploid, mostly triploid ($3x = 12$), rarely tetraploid ($4x = 16$), or even pentaploid ($5x = 20$) (Benazzi 1982). However, they do not differ in copulation behavior: sexuals as well as parthenogens mate and exchange sperm reciprocally (Michiels and Bakovski 2000; Michiels and Kuhl 2003). Copulation is necessary in parthenogens because they are sperm-dependent (sperm-dependent parthenogenesis or pseudogamy, Beukeboom and Vrijenhoek 1998) and require allosperm to trigger zygote division and embryo development. Nevertheless, there is usually no paternal genetic distribution to the offspring as paternal alleles either degenerate within the zygote or are expelled with one of the polar bodies (Benazzi Lentati 1970). As sperm-dependent parthenogenetic *S. polychroa* still retain functional male organs, they are independent of sexual sperm donors in purely parthenogenetic populations.

Parthenogens produce polyploid eggs. However, in some parthenogenetic biotypes polyploid eggs originated via mitosis (reported for tetraploids and triploids) in other biotypes meiotically after chromosome duplication (reported only for triploids) (Benazzi Lentati 1970). Spermatogenesis in parthenogens proceeds meiotically after

chromosome set elimination (one in triploids and 2 in tetraploids). The resulting spermatocytes are haploid and fertile. Sperm of parthenogens can therefore fertilize eggs of sexual mating partners (Benazzi 1963; Benazzi Lentati 1970; Storhas et al. 2000). New parthenogenetic lineages sometimes arise from such matings (Benazzi Lentati 1970).

Although parthenogenetic (polyploid) biotypes do reproduce occasionally via sexual means (see below), we still refer to them as parthenogens and not as sexuals to avoid confusion with obligate sexual (diploid) biotypes.

Sex Versus Asex in *S. polychroa*

The distribution of sexual and parthenogenetic biotypes follows the classical pattern of geographic parthenogenesis (Lynch 1984). Sexuals only occur south of the Alps (with the exception of Southern Sweden, Melander 1963), whereas parthenogens are distributed across most of Europe. Consequently, parthenogens occur in mixed populations in southern Europe and exclusively parthenogenetic populations occur elsewhere (Beukeboom et al. 1996; Pongratz et al. 1998, 2003).

The cost of sexual reproduction in *S. polychroa* becomes clear when studying the investment into male and female function. Compared with sexuals, parthenogens show reduced male allocation, which saves resources for other functions (Weinzierl et al. 1998). This may lead to the observed increased production of cocoons in parthenogens (Weinzierl et al. 1999). However, female fertility is strongly reduced in parthenogens (Weinzierl et al. 1999; Storhas et al. 2000). Moreover, parthenogens suffer from high embryo mortality, which is presumably caused by the accumulation of deleterious mutations (Storhas et al. 2000; Storhas 2001). Parthenogens show on average higher infection rates compared with coexisting sexuals and interclonal variation in parasite load (Michiels et al. 2001). Both findings are consistent with at least some of the predictions of the Red Queen hypothesis (e.g., Neiman and Koskella 2009).

Moreover, according to the pluralistic approach, which combines the effects of mutation-based and parasite models for explaining the maintenance of sex (West et al. 1999), clonal lineages with increased embryo mortality are also more heavily infected by parasites (Bruvo et al. 2007). The data thus far suggest that parthenogens indeed suffer from both the accumulation of deleterious mutations and elevated susceptibility to parasites, with synergistic effects possibly amplifying both. Nevertheless, parthenogens remain geographically more widespread and dominant than their sexual conspecifics.

Occasional Sex in Parthenogenetic *S. polychroa*

The key benefit of sperm-dependent parthenogenesis is the option of obtaining paternal fitness by fertilizing eggs as a male. Although sperm from parthenogens can fertilize eggs from sexual mating partners (Benazzi Lentati 1970; Storhas et al. 2000), here we concentrate on processes acting on purely parthenogenetic populations only. For a more extensive review including gene flow between parthenogens

and sexual *S. polychroa* and its evolutionary consequences see D'Souza and Michiels (2009).

Sex among parthenogens has been shown with paternity analysis for individuals mated in the field (D'Souza et al. 2004) and for controlled crosses in the laboratory (D'Souza et al. 2006) and can take different forms that may or may not involve ploidy alternations. In all types, haploid sperm fuses with a parthenogenetic egg but without subsequent elimination of paternal chromosomes (Figure 1). This process allows paternal genes to “leak” into the next parthenogenetic generation. A ploidy change follows when haploid sperm is incorporated into a triploid egg, giving rise to a tetraploid offspring (A in Figure 1). Tetraploids can in turn produce triploid offspring. This requires the production of reduced, diploid eggs that are fertilized by haploid sperm (B in Figure 1). Through the 2-step cycle from the common triploid forms to the rare tetraploids and back, triploid genomes effectively recombine through the production of tetraploids (D'Souza et al. 2004). Other known forms of occasional sex do not involve a change in ploidy but are based on a one-step mechanism in which a maternal chromosome set is substituted by the incorporated paternal set. The result is that triploid mothers sometimes produce triploid offspring with 2 maternal and one paternal chromosome set (C in Figure 1). The same process can be observed in tetraploids. We estimated that 5–12% of all offspring produced in a purely parthenogenetic population arise via one of these mechanisms (D'Souza et al. 2004, 2006).

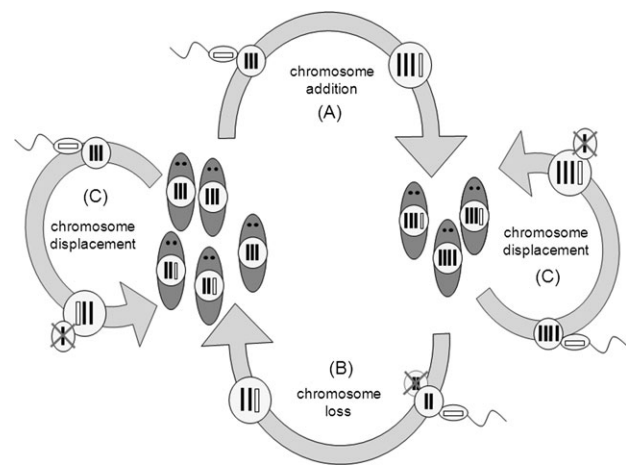


Figure 1. Mechanisms of occasional sex in *Schmidtea polychroa*. Black and gray bars represent maternal and paternal chromosome sets, respectively. The number of bars reflects the ploidy level in egg, sperm, zygote, and soma. Sexual processes in parthenogenetic *S. polychroa* may include a 2-step cycle with ploidy changes (chromosome addition (A) plus chromosome loss (B)) or a one-step cycle with ploidy restoration (chromosome displacement (C)). In all cases haploid sperm fertilizes polyploid eggs without being subsequently expelled from the zygote and hence contributes genetically to the offspring.

Interestingly, the degree of sex seems to vary across subpopulations as can be derived from population genetics (D'Souza and Michiels 2006). Such variation is unique and useful as it makes it possible to test the consequences of different levels of sex at the population level among otherwise absolutely identical biotypes.

Costs of Occasional Sex in *S. polychroa*

Sperm-dependent parthenogenetic *S. polychroa* do not only rely on sperm donors in order to reproduce, they are also still hermaphrodites and hence invest in male organs and sperm production. Requiring sperm for offspring production is problematic in purely parthenogenetic populations as sexual sperm donors are missing. A mutant allocating all resources to the female function will gain a clear fitness advantage over the residents and increase in frequency. Hence, parthenogenetic populations may become extinct due to a lack of sperm donors. Maintaining an albeit small, residual male function is thus essential for long-term survival of sperm-dependent parthenogenetic populations and represents costs parthenogenetic *S. polychroa* are faced with, independent of occasional sex per se. However, investing into functional and fertile sperm is a prerequisite for sex in parthenogenetic *S. polychroa* and is also associated with sex, as we will see later.

As described above, tetraploids represent a crucial intermediate for occasional sex in parthenogenetic *S. polychroa*. However, the production of tetraploid offspring is costly as tetraploids produce fewer offspring than triploids (D'Souza et al. 2005). The reduced fitness of tetraploids is caused by decreased cocoon production and is independent of the number of offspring per cocoon. Moreover, triploids and tetraploids do not differ in other traits, such as body size or embryo development (D'Souza et al. 2005). Hence, the reduced cocoon production of tetraploids is the major cost of occasional sex in *S. polychroa*.

Importantly, the local presence of tetraploidy can be used as an indicator for occasional sex as it not only emerges but is also maintained by occasional sex. Given the fitness difference between the ploidy types, triploids would displace tetraploids within a few generations. However, occasional sex with its recurrent generation of tetraploids prevents their local extinction and leads to stable coexistence between both ploidy types (D'Souza et al. 2005). In the same line of argumentation, tetraploid frequency is a good and reliable proxy for the degree of sex as it is strongly correlated with genotypic diversity of triploids (D'Souza and Michiels 2006, 2008).

Benefits of Occasional Sex in *S. polychroa*

An immediate consequence of sexual reproduction is the generation of genetic and genotypic diversity by shuffling genomes (e.g., Agrawal 2006). Comparably, occasional sex leaves telltale population genetic signatures in genotypic diversity and evenness that coincide with different amounts of occasional sex in *S. polychroa* (D'Souza and Michiels 2006).

Clonal diversity is important as it allows a parthenogenetic population to respond more dynamically to changing environments (e.g., Sasaki et al. 2002). Genotypic diversity inferred from microsatellites is high in parthenogens and may reach values typical for sexual populations (Storhas 2001; D'Souza and Michiels 2006). Significant interclonal variation has been described for several traits, such as male allocation and fertility (Storhas 2001), offspring number, fecundity, body size, and hatching time (D'Souza et al. 2005; D'Souza and Michiels 2008). This indicates that clones are of different ages and hence have accumulated different amounts of deleterious mutations and/or that clones follow different ecological strategies and occupy different micro-niches. The latter supports the idea of the frozen niche variation hypothesis to explain the maintenance of clonal diversity (Vrijenhoek 1998; Jokela et al. 2003).

One important precondition of occasional sex in exclusively parthenogenetic populations is the production of fertile sperm. Comparing individuals from a highly clonal location and a location with occasional sex, sperm length measurements revealed significantly smaller sperm where occasional sex is absent (D'Souza et al. 2008). We propose this is due to reduced sperm competition or degeneration of sperm caused by accumulation of deleterious mutations. The effect of sperm quality was studied with crossings within each location and between the 2 locations, whereas the number of offspring per cocoon was used as an indicator of the partners' sperm quality. Sperm from the clonal location fertilized fewer eggs and therefore sired fewer offspring per cocoon than sperm from the more sexual location. Interestingly, sperm rather than egg quality determines fertility (D'Souza et al. 2008). This suggests that occasional sex selectively favors better ejaculates through sperm quality and/or quantity. Importantly, occasional sex also allows male traits, like sperm quality/quantity to be subject to selection. Hence, occasional sex itself creates and amplifies its prerequisite.

The crucial bottom line is that occasional sex eventually increases the fitness of parthenogenetic (sub-)populations: tetraploid frequency, used as a proxy for the degree of rare sex in a population, correlated positively with fitness variance across 6 subpopulations of the same lake. Due to increased variability, selection may act more effectively, which explains that subpopulations with a higher degree of sex also had highest mean fitness (D'Souza et al. 2008). In this study, fitness estimates of the subpopulations only considered triploid individuals as triploidy represents the initial status of parthenogenesis in *S. polychroa* and excludes any confounding effect of ploidy variation. Hence, we focused on the benefits of occasional sex only. Including tetraploid fitness in the analysis allows a cost–benefit analysis of occasional sex (previously unpublished).

Evaluating the Costs and Benefits of Occasional Sex in *S. polychroa*

The degree of sex is not only positively correlated with the mean fitness of the subpopulations comprising triploids

only (D'Souza et al. 2008, Spearman rank correlation, $n = 6$, $r_s = 0.886$, $P = 0.019$, dotted line in Figure 2) but also with the subpopulations' overall fitness (Spearman rank correlation, $n = 6$, $r_s = 0.876$, $P = 0.002$, solid line in Figure 2). Importantly, the latter also accounts for the major costs of occasional sex, namely the reduced fitness of tetraploids and hence represents the net benefits of occasional sex. The costs of occasional sex a subpopulation has to pay can then be quantified by subtracting the triploid fitness from the overall fitness (note that other potential costs of occasional sex are not included in this calculation). The resulting costs (dashed line in Figure 2) are also significantly, positively correlated with the degree of sex (Spearman rank correlation, $n = 6$, $r_s = 0.886$, $P = 0.019$). The more tetraploids are present in a subpopulation the stronger their (negative) contribution to the overall fitness.

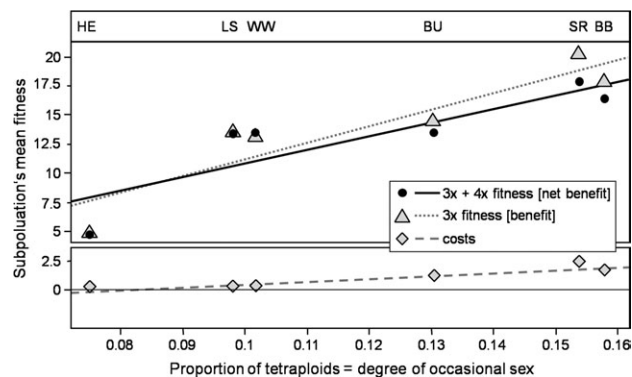


Figure 2. Costs and benefits of occasional sex at a population level: Names of the sampling locations are given at the top of the figure (HE Herrsching, LS Lochschwaben, WW Wartaweil, BU Buch, SR Schloß Ried, and BB Breitbrunn). For all locations, which are situated at the east shore of the lake Ammersee, Southern Germany, proportion of tetraploids has been determined as a proxy for the degree of occasional sex. Fitness was estimated as the offspring number individuals produced within 35 days. Subpopulation's mean fitness of the subpopulations was calculated per location for only triploids (triangles) and for triploids and tetraploids (circles). In both cases, proportion of tetraploids correlates significantly and positively with triploid fitness (Spearman rank correlation, $n = 6$, $r_s = 0.886$, $P = 0.019$, dotted line) and triploid + tetraploid fitness (Spearman rank correlation, $n = 6$, $r_s = 0.876$, $P = 0.002$, solid line). Regression lines has been included for illustrational and not for statistical purpose. As triploid + tetraploid fitness also includes the cost of occasional sex, namely the reduced fitness of tetraploids, it represents the net benefit of occasional from which the actual costs of occasional sex can be calculated. Subtracting the triploid fitness from triploid + tetraploid fitness per location reveals a cost estimate each location has to pay for its degree of occasional sex (diamonds). With increasing rate of sex, the costs are also rising (Spearman rank correlation, $n = 6$, $r_s = 0.886$, $P = 0.019$, dashed line).

In summary, these results suggest that the benefits of occasional sex clearly outweigh its costs, which may explain the success and dominance of parthenogenesis in *S. polychroa*.

Discussion

If occasional sex is indeed as advantageous as 100% sex, one may ask why it is not more common. There are 2 possible answers to this question: 1) rare sex is evolutionary unstable or 2) many organisms actually do combine sex and asex and it is currently unobserved.

In the long-term rare sex may lead to either obligate sex or obligate asex (Hurst and Peck 1996; Peck and Waxman 2000). Under heterozygote advantage, a mixed reproduction mode may evolve to obligate asex when sexual processes become too rare and hence the benefits of sex vanish (Peck and Waxman 2000). Moreover, the fate of partial sexuality is condition dependent (Peck et al. 1997; Rispe and Pierre 1998; Scheu and Drossel 2007). Population size, number of loci under selection, and stability of the environment strongly determine the benefits of partial sexuality compared with obligate reproductive modes (Peck 1996; Peck et al. 1997). Once the sex rate is increased the reversion to asexuality may be hindered (Hurst and Peck 1996; Engelstadter 2008, but see Delmotte et al. 2001; Simon et al. 2003). Such a block to asexuality, for example, caused by imprinting in mammals, would explain the high frequency of obligately sexual species.

In *S. polychroa*, we found that the rate of sex is variable among populations and at least in some cases also across time (D'Souza and Michiels 2006, 2008). This spatial and temporal variability may suggest that the observed sex rate is eventually the result of adaptations to the local characteristics of the population characteristics (e.g., overall mutation load and environmental fluctuations). In the same line of argumentation, populations would then be able to plastically adjust the population's level of sex to the specific local environmental regime, which may explain why the sex rate is still always low and never reaches high magnitudes comparable with fully sexual reproduction. However, making statements on whether the observed sex rates are optimal sex rates would be too speculative at the moment and clearly needs further investigations.

Furthermore, very little information is available about the number of species that combine sex and asex. Sexual processes in parthenogenetic species are often difficult to detect as they are often infrequent (Schurko et al. 2009) or occur in response to a certain, likely unknown, environmental stimulus (Dacks and Roger 1999). Additionally, sexual processes are often cryptic and proceed in an unpredictable fashion (e.g., Hurst et al. 1992). However, in the course of advanced molecular and cytogenetics, more and more examples of occasional sex in presumably asexual species may arise (Schurko and Logsdon 2008; Schurko et al. 2009). For instance, nearly all protists are facultative parthenogens (Dacks and Roger 1999) and there is increasing incidence for facultative asexual metazoans. The

existence of 100% obligate apomicts has been questioned, especially in plants (Asker and Jerling 1992). Most sexual plants have the capability of vegetative reproduction and most apomictic plants retain at least some degree of sexuality (Asker and Jerling 1992; Richards et al. 2003; Honnay and Bossuyt 2005). Many parthenogenetic animals show some form of rare, sexual mixing (e.g., Goddard and Schultz 1993; Schartl et al. 1995; Belshaw et al. 1999; Delmotte et al. 2001; Schurko et al. 2009). With the increasing incidence of rare sex in parthenogenetic animals, it is also likely that purely clonal reproduction is restricted to only few species, for example, ancient asexuals. Hastings (1992) therefore concluded “obligate sex observed in large metazoa is an evolutionary oddity and that life cycles that involve occasional sex are the norm.”

In fact, all metazoans can be regarded as a rare sex system, if we change the perspective from individuals as reproductive units to individual cells (or individual alleles) of multicellular organisms. Within the germ line, multiple rounds of mitotic (asexual) divisions are followed by meiosis and sexual recombination. Hence, each gamete is the result of a sexual/asexual life cycle, which combines the advantages of both systems (Hastings 1991).

That being said, a lot more empirical and theoretical investigation is necessary to study the incidence and evolutionary advantages of occasional sex. First, we need a better understanding of the actual costs of a mixed reproductive mode. What costs do asexuals experience by retaining residual capability of sex, that is, investment in male function? Although many theoretical studies reveal advantages of rare sex, empirical confirmation is scarce. Competition experiments between obligate and mixed reproduction modes will give important insights into the benefits of occasional sex. Including sexual selection and synergism of classical theories of sex will further complete the picture and help to answer questions about how much sex is really necessary. With this information, we are starting to understand why such a wide variety of different reproductive modes exist.

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