

Using Parthenogenetic Lineages to Identify Advantages of Sex

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Abstract The overwhelming predominance of sexual reproduction in nature is surprising given that sex is expected to confer profound costs in terms of production of males and the breakup of beneficial allele combinations. Recognition of these theoretical costs was the inspiration for a large body of empirical research—typically focused on comparing sexual and asexual organisms, lineages, or genomes—dedicated to identifying the advantages and maintenance of sex in natural populations. Despite these efforts, why sex is so common remains unclear. Here, we argue that we can generate general insights into the advantages of sex by taking advantage of parthenogenetic taxa that differ in such characteristics as meiotic versus mitotic offspring production, ploidy level, and single versus multiple and hybrid versus non-hybrid origin. We begin by evaluating benefits that sex can confer via its effects on genetic linkage, diversity, and heterozygosity and outline how the three classes of benefits make different predictions for which type of parthenogenetic lineage would be favored over others. Next, we describe the type of parthenogenetic model system (if any) suitable for testing whether the hypothesized benefit might contribute to the maintenance of sex in natural populations, and suggest

groups of organisms that fit the specifications. We conclude by discussing how empirical estimates of characteristics such as time since derivation and number of independent origins of asexual lineages from sexual ancestors, ploidy levels, and patterns of molecular evolution from representatives of these groups can be used to better understand which mechanisms maintain sex in natural populations.

Keywords Asexuality · Parthenogenesis · Meiosis · Sexual reproduction

Introduction

Sexual reproduction is associated with profound costs relative to asexuality and other forms of thelytokous (female-producing) parthenogenesis. A sexual female only transmits half of her genome to each offspring, and she produces both sons and daughters. Since only females can directly produce offspring, the difference between sexual and parthenogenetic females in the rate of daughter production translates into a twofold cost of sex (Maynard Smith 1978). This cost is manifested in the dramatically slower growth rate of the sexual population caused by allocation to sons instead of daughters. Thus, if all else is equal between the two types of females, sexual lineages should lose in direct competition with parthenogenetic lines. This effect should be further enhanced by additional costs of sex, such as the breakup of co-adapted gene complexes, or more taxon-specific costs associated with mate location or mating itself. The overwhelming predominance of obligate sex in nature thus means that sexual reproduction must confer benefits so profound that they fully counter these multifaceted costs (Williams 1975; Maynard Smith 1978; Bell 1982).

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Theoreticians have used analytical and simulation models to identify many possible advantages of sexual reproduction, from the clearance of harmful mutations to decreased competition between siblings to more effective evolutionary responses to natural selection. Within the limits of their assumptions, many of these theoretical models are able to show twofold advantages of sex (Kondrashov 1993; Otto 2009). However, the question at hand is not whether the models can maintain sex, but rather, what mechanisms in fact favor obligate sex in natural populations. Despite decades of study, the answer remains unclear (recently reviewed in de Visser and Elena 2007; Hadany and Comeron 2008; Otto 2009).

Thus far, the maintenance of obligate sexuality in nature has mainly been addressed by contrasting sexual with related asexual lineages (e.g., Pongratz et al. 2003; Wolinska and Lively 2008; Neiman et al. 2010). Here, we suggest that new insights into the advantages and maintenance of obligate sexuality in natural populations can come from identifying how different classes of parthenogenetic lineages are expected to perform under different hypotheses for sex and empirically evaluating these predictions.

Parthenogens differ in three aspects that are useful for evaluating theoretical advantages of sexual reproduction. First, many different cytological and developmental processes can underlie the production of eggs (Fig. 1). Notably, certain modes of parthenogenesis function without recombination and segregation (i.e., mitotic parthenogenesis) while others maintain meiosis either partly or completely. Among meiotic parthenogens, there is further variation with respect to how meiosis is modified to produce eggs with somatic ploidy levels instead of haploid gametes. This variation affects the distribution of genetic variance within and among individuals (Fig. 1). Thus, comparing all-female lineages employing different modes of parthenogenesis may allow tests for predicted advantages of recombination and genetically variable offspring in the absence of other costs of sex.

Second, many parthenogenetic taxa are represented by lineages with different ploidy levels. Such systems allow tests of hypotheses relating to the accumulation and phenotypic effects of mutations, because an increase in ploidy level can affect both the mutation rate and the expression of mutational effects (e.g., Richards 1997; Otto and Whitton 2000). Finally, what is treated as a single parthenogenetic species can either represent a single transition from sexuality to parthenogenesis or consist of an assemblage of independently derived, genetically diverse lineages (recently reviewed in Neiman et al. 2009). These two groups can be used to assess models for the advantage of sex that rely on intra-population genetic variation, such as models based on negative frequency-dependent selection.

In our review, we first outline the major classes of the predicted advantages of sex. We then describe the type of parthenogenetic model system (if any) suitable for testing whether the hypothesized benefit might contribute to the maintenance of sex in natural populations. Whenever possible, we suggest groups of organisms that fit the specifications for each type of hypothesis and summarize the insights that can come from using such systems for research directed at understanding the benefits of sex (Table 1).

Predicted Advantages of Sex and how to Use Parthenogenetic Systems to Study Them

The problem of sex has attracted a great deal of theoretical interest (see Kondrashov 1993, also recently reviewed in Otto 2009) since George Williams and John Maynard Smith pointed out that sex is so costly that its maintenance requires profound and rapidly generated individual-level advantages (Maynard Smith 1971, 1978; Williams 1971, 1975). This realization led to the rejection of the long-held belief that sex is maintained because of its ability to rapidly combine beneficial alleles segregating at different loci within a population (Fisher 1930; Müller 1932), and highlighted that even profound advantages of sex may not in fact explain its maintenance. A new quest to identify more rapidly-operating advantages of sex and characterize their presence in nature began, and continues to this day.

Most recent reviews of potential advantages of sex have followed Kondrashov (1993) in classifying hypotheses for sex into “environmental” versus “mutational” classes depending upon whether the agent of selection favoring sex comes from changing environments or from mutation pressure (e.g., Rice 2002). In the context of our review, however, a different classification scheme is more useful. Here, we will classify hypotheses for sex based on whether they involve mechanisms that generate advantages linked directly to the breakup of allelic combinations (“linkage” hypotheses), advantages of genetic diversity or genotypic rareness (“diversity” hypotheses), or advantages of heterozygosity (“heterozygosity” hypotheses). We will then discuss the particular mode of parthenogenesis or types of parthenogens that can or cannot realize the specific benefits of sex. For example, the advantages of genotype diversity can often be achieved via all types of parthenogenesis as long as asexual assemblies are very diverse, while linkage hypotheses require either meiotic parthenogenesis or sex. Whether parthenogenetic lineages can realize the benefits of heterozygosity-based hypotheses depends both on the particular mode of parthenogenesis and ploidy level.

Fig. 1 The major parthenogenesis modes in animals and their consequences for the maintenance of heterozygosity and genetic variation among offspring. The different parthenogenesis modes and their consequences for single-locus homozygosity were first reviewed by Suomalainen et al. (1987), and subsets of these modes have been reconsidered recently by Pearcy et al. (2006) and Stenberg and Saura (2009). An exhaustive list, including modes that could theoretically exist but have not been described in living organisms, is presented in Archetti (2010). Here, we only consider parthenogenesis modes known from real organisms. We follow the classification by Suomalainen et al. (1987). Each parthenogenetic lineage typically uses a single mode of parthenogenesis; however, more than one mode may occur within sets of lineages lumped together taxonomically into a single “parthenogenetic species”. For each parthenogenesis mode, we indicate the expected proportion of all possible offspring genotypes for a single locus at which the mother was heterozygous (genotype A1/A2), depending on whether a recombinational event occurred between the locus and the centromere

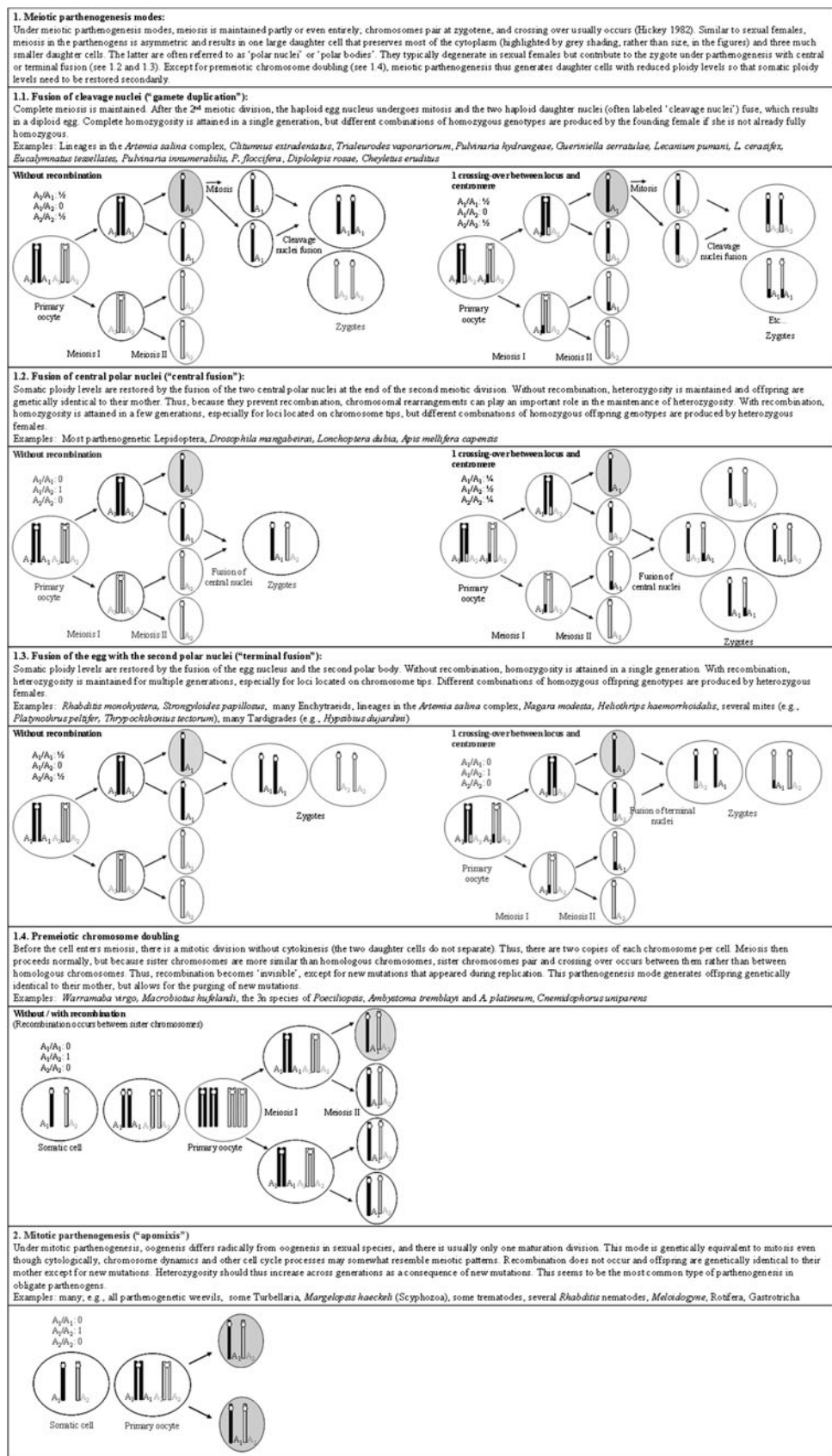


Table 1 A list of important hypothesized benefits of sex, predicted differences between particular types of parthenogens under each of these hypotheses, and examples of taxa that can be used to evaluate whether these predictions are met

Benefit of sex	Predictions	Type of parthenogen ^a	Examples of suitable taxa
Mutational clearance	1	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
	2	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
Mutational assembly	NA	None	NA
Increased efficacy of selection on beneficial mutations	3	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
	4	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
Generation of diversity	5	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
	6	NA	NA
	7	Closely-related lineages with variable ploidy levels and same parthenogenesis mode	<i>Potamopyrgus antipodarum</i> snails, <i>Schmidtea polychroa</i> flatworms
Maintenance of heterozygosity	8	Closely-related mitotic and meiotic lineages	<i>Artemia salina</i> complex, <i>Meloidogyne</i> root knot nematodes
	9	Closely-related hybrid versus non-hybrid lineages with the same parthenogenesis mode	<i>Campeloma</i> snails
	10	Closely-related meiotic parthenogens with variable parthenogenesis modes	

NA not applicable

1 Higher rate of mutation accumulation in mitotic parthenogens

2 Relatively old age of meiotic versus mitotic parthenogens

3 Evidence for more effective positive selection in DNA sequence from meiotic versus mitotic parthenogens

4 More rapid response to positive selection in meiotic versus mitotic parthenogens

5 Evidence for more effective positive/balancing selection in meiotic versus mitotic parthenogens

6 Higher mean lineage age in multi- versus single-origin parthenogens

7 Higher mean lineage age of polyploid versus diploid taxa with the same mode of parthenogenesis

8 Higher mean lineage age in mitotic versus meiotic parthenogens

9 Higher mean lineage age of hybrid versus non-hybrid taxa with the same mode of parthenogenesis

10 Higher mean lineage age of meiotic parthenogenetic types where heterozygosity is lost more slowly

^a If there do not exist closely-related taxa with the desired characteristics, one could instead perform a comparative analysis across lineages from independent taxa

Linkage Hypotheses

What unites linkage-based mechanisms for sex is that they all generate advantages via the breakup of linkage disequilibrium (LD), non-random associations between alleles at different loci. The disruption of LD allows alleles to experience selection independently of their genetic background (reviewed in Felsenstein 1974; Felsenstein and Yokoyama 1976; Otto 2009). The predictions of LD-based models diverge depending on whether they are based on finite or infinite populations. Since we focus on the maintenance of sex in natural populations, and since empirical data suggest that most natural populations are far from infinite (reviewed in Hastings and Harrison 1994; Wade and Goodnight 1998; Hadany and Comeron 2008), we here only consider only those mechanisms that apply to finite populations.

LD breakup is a consequence of meiotic recombination and segregation. Since effective population size (N_e) is reduced by genetic linkage (Robertson 1961; Hill and Robertson 1966; Birky and Walsh 1988), and since the efficacy of selection decreases with N_e (Wright 1931; Crow and Kimura 1970; Ohta and Kimura 1971), sex is predicted to be associated with more effective clearance of harmful mutations and more rapid spread of beneficial mutations (Felsenstein 1974; Felsenstein and Yokoyama 1976; Birky and Walsh 1988; reviewed in Hadany and Comeron 2008). These advantages for sex have all been recently and thoroughly reviewed (e.g., de Visser and Elena 2007; Hadany and Comeron 2008; Otto 2009), so we will provide only a brief, conceptually-focused overview.

Linkage among loci can result in the accumulation of slightly harmful mutations through different population

genetic processes. One set of processes refers to the repeated loss of the class of individuals with the fewest deleterious mutations (“Muller’s Ratchet”), which may lead to extinction of the asexual lineage (Muller 1964; Lynch et al. 1993). Another set of processes refers to the reduced efficacy of purifying selection experienced by harmful mutations that are tied to a fixed genetic background (“Hill-Robertson effect”; Hill and Robertson 1966; Felsenstein 1974; Pamilo et al. 1987; Charlesworth et al. 1993). Recombination can retard both of these processes by regenerating individuals with a lower mutational load under Muller’s ratchet and also by decreasing LD and thus increasing the efficiency of purifying selection (reviewed in Neiman and Taylor 2009). This is the logic underlying the expectation that sexual lineages should have a decreased rate of accumulation of harmful substitutions relative to recombination-free lineages.

In line with this expectation, asexual lineages do seem to be characterized by higher rates of accumulation of presumably harmful mutations than their sexual counterparts (Normark and Moran 2000; Paland and Lynch 2006; Johnson and Howard 2007; Neiman et al. 2010). However, it is often difficult to exclude the possibility that other processes generate these differences. Notably, less effective and/or relaxed purifying selection due to factors such as differences in census population sizes or the strength and direction of selection could generate similar patterns, particularly when sexual and asexual lineages do not coexist and/or are only distant relatives. However, as Maynard Smith (1978) and others (Suomaleinen 1950; Bierzychudek 1985) pointed out, the fact that even relatively closely-related sexual and asexual taxa often inhabit different types of habitats or produce different types of eggs (such as diapausing vs. non-diapausing eggs), means that our ability to disentangle the effects of sex from other mechanisms using sexual/asexual comparisons is often severely limited.

There are two ways that we can use parthenogenetic lineages to more directly evaluate whether the accumulation of deleterious mutations limits asexual persistence. First, similar to sexual: asexual comparisons, rates of deleterious mutation accumulation can be compared between meiotic and mitotic parthenogens. Because they maintain recombination and segregation, meiotic parthenogens are predicted to harbor fewer deleterious mutations than mitotic types (Browne 1992; Haccou and Schneider 2004). This prediction should hold even if recombination rates appear to be very low in meiotic parthenogens, since simulation-based studies have found that very little recombination—perhaps even below detectable limits (Neiman and Taylor 2009)—is required to achieve substantial mutational clearance (Pamilo et al. 1987; Charlesworth et al. 1993; Green and Noakes 1995). In fact, the observation that meiotic parthenogenesis is often

associated with low hatching success or juvenile survival (Templeton 1982; Schwander et al. 2010) might provide indirect support for the possibility that this type of parthenogenesis facilitates mutational clearance. While these patterns likely stem from homozygosity at recessive deleterious alleles, incompatible epistasis effects, and other mechanisms underlying inbreeding depression (Templeton 1982; Kramer and Templeton 2001; Schwander et al. 2010), they also reveal the potential for selection to remove deleterious mutations in these lineages in a manner analogous to the purging of mutational load that can be a consequence of inbreeding depression.

Second, if the accumulation of deleterious mutations limits asexual persistence, lineages with meiotic parthenogenesis should be more persistent than mitotic parthenogens. In a comparative approach, the fraction of mitotic parthenogens should therefore decrease with increasing ages of the lineages and the oldest lineages should tend to use meiotic parthenogenesis. This is the basis for our argument that support for sex being maintained in natural populations because it facilitates mutational clearance would come from meiotic parthenogens having lower rates of accumulation of harmful mutational types and persisting longer than their mitotic counterparts in each of these groups.

Taxon groups that are represented by both naturally-occurring meiotic and ameiotic parthenogens and that can thus be used to evaluate these predictions include but are not limited to the *Artemia salina* brine shrimp complex, *Meloidogyne* root knot nematodes, Coccids, tardigrades and *Schmidtea polychroa* flatworms (Supplemental Table 1).

We were not able to evaluate the extent to which the mutational accumulation prediction is met because the degree of mutation accumulation has not been evaluated in any of these groups. While age distributions for parthenogenetic lineages have recently been reviewed by Neiman et al. (2009), the lack of data for most groups (Supplemental Table 1) and the uncertainties associated with most age estimates do not yet allow for meaningful assessment of changes in the relative frequency of mitotic parthenogens across different lineage age classes.

Linkage among loci can also reduce the efficiency of selection on beneficial mutations, such that the breakup of LD should facilitate their spread. There are two ways in which this can occur. First, as for deleterious mutations, recombination will free individual beneficial mutations from selective interference imposed by the genetic background (Hill and Robertson 1966; Felsenstein 1974; Felsenstein and Yokoyama 1976; Barton and Otto 2005; Keightley and Otto 2006). Similar to the removal of deleterious mutations, this mechanism should thus give an advantage to meiotic parthenogens. In this case, one would predict that positive selection should proceed more efficiently in meiotic versus mitotic parthenogens. Such a

discrepancy in the efficacy of positive selection could be addressed by comparing patterns of molecular polymorphism and substitution in closely-related mitotic and meiotic parthenogenetic lineages (Table 1).

It is important to note that there exist some linkage-based hypotheses that cannot be tested with parthenogens because they involve mechanisms that are unique to sex. For example, theory suggests that because recombination and amphimixis can combine novel beneficial alleles in the same lineage (“mutation assembly”), they can, under some conditions, maintain sex and relatively high rates of recombination (Fisher 1930; Müller 1932; Felsenstein 1974; Felsenstein and Yokoyama 1976; Otto and Barton 1997; Roze and Barton 2006). Because there is no genetic exchange between individuals under any type of parthenogenesis, possible benefits of sex from this mechanism cannot be evaluated using parthenogenetic lineages.

Diversity Hypotheses

Diversity-based mechanisms operate by generating advantages for individuals with rare genotypes. For example, in many host-parasite coevolution models, infection probability is assumed to be genotype specific, i.e., specific host genotypes are susceptible to specific parasite genotypes. Here, theory suggests that disproportionately high infection rates in common asexual lineages could favor the genetically diverse sexual individuals and allow for the coexistence of sexual and asexual lineages (reviewed in Neiman and Koskella 2009). Recent empirical data are consistent with this possibility (Decaestecker et al. 2007; Jokela et al. 2009).

Resource limitation can also set the stage for a scenario where relatively rare genotypes are more successful (Williams and Mitton 1973; Williams 1975). For example, if the environment is saturated and genetic differences are associated with differences in niche exploitation, genetic diversity can reduce competition among siblings and allow for the exploitation of less occupied niche space. In this case, sex could be favored because it generates offspring that differ from each other and from other individuals in the population (reviewed in Bell 1982; Burt 2000). Producing genetically variable offspring can also be a bet-hedging strategy in highly variable environments (Williams 1975; Bell 1982).

Under diversity hypotheses, sex is favored not because of the consequences of processes unique to sexual reproduction but because it is associated with the production of genetically diverse progeny. In fact, theory suggests that the advantage of sex will decrease as the diversity of coexisting asexual lineages increases, to the extent that the maintenance of sex cannot be explained by negative frequency-dependent selection when the diversity of asexual

assemblages equals that of the sexuals (reviewed in Lively 2010). This is the basis for our prediction that if diversity-based mechanisms are important for the maintenance of sex, parthenogenetic assemblages consisting of independently-derived (and thus genetically heterogeneous) lineages should be more persistent than single-origin lineages (see also Maynard Smith 1978).

While these predictions are conceptually straightforward, they may be difficult to evaluate. For example, the number of independent origins of lineages within a parthenogenetic clade or within a mixed sexual/asexual taxon is difficult to infer (Judson and Normark 1996). Such inferences become especially difficult as the ages of the parthenogenetic lineages increase, in part because the parthenogens might have driven their sexual ancestors to extinction. For example, in the bdelloid rotifers, which stand as the most prominent example of ‘ancient asexuality’, it is impossible to determine with confidence whether ecologically divergent clusters of asexual ‘species’ represent diversification after the transition to asexuality (which is typically assumed, see Fontaneto et al. 2007) versus multiple independent transitions to asexuality but where the sexual ancestors are now extinct. While there are challenges associated with evaluating diversity hypotheses from a phylogenetic or comparative perspective, experimental approaches may prove more productive. For example, the demographic success of a lineage under monoculture versus diverse conditions (e.g., Tagg et al. 2005) could provide important insights into the extent to which diversity per se might provide an advantage to sexual reproduction.

Heterozygosity Hypotheses

The loss of heterozygosity has been postulated to be a major constraint for the evolution of asexuality because it increases the likelihood of expression of recessive deleterious mutations (Maynard Smith 1978; Suomalainen et al. 1987; Archetti 2010). Most types of meiotic parthenogenesis are associated with rapid loss of heterozygosity (Fig. 1). By contrast, heterozygosity is expected to be maintained under mitotic parthenogenesis. The implications are that the loss of heterozygosity may constrain the evolution of meiotic parthenogens, but not mitotic ones, in situations where they are competing with sexuals.

The proximate factors explaining the correlation between overall heterozygosity and fitness (e.g., Spurgin and Richardson 2010) are typically elusive. Resistance to parasites (Hamilton and Zuk 1982) represents a possible mechanism, either because inbreeding depression compromises individual ability to control infection (e.g., Morris and Harrison 2009), or because heterozygous individuals have a broader array of pathogen resistance (Coltman et al. 1999;

Ortego et al. 2007). The most often cited example in this context is heterozygosity at the MHC complex in vertebrates. Indeed, the clearance of an infection generally proceeds faster in MHC heterozygotes than in homozygotes (e.g., Thursz et al. 1997; Carrington et al. 1999) and MHC heterozygotes are typically overrepresented in natural populations (e.g., Hedrick and Thomsom 1983; Black and Hedrick 1997). As for overall heterozygosity level, however, the relationships between MHC diversity and host resistance to pathogens are complex and remain unclear, as do the physiological and immunological mechanisms driving these relationships (Woelfing et al. 2009; Spurgin and Richardson 2010).

Even in the absence of definitive characterization of why high heterozygosity is associated with high fitness, we can still use parthenogenetic lineages to perform meaningful tests of the extent to which links between sex and the maintenance of heterozygosity might contribute to the maintenance of sex. First, we can evaluate whether old parthenogenetic lineages are characterized by high levels of polyploidy. Polyploidy is expected to provide temporary protection from the expression of recessive deleterious alleles because these alleles will be shielded for some time by the presence of extra wildtype alleles (Otto and Whitton 2000). Second, because the transition to homozygosity is slower under mitotic than meiotic parthenogenesis, mitotic parthenogens should be more persistent than meiotic types. Thus, within a given ploidy level, mitotic parthenogens should become overrepresented among older lineages. Third, because heterozygosity should be particularly high in hybrids, parthenogens that originated from hybridization between sexual species should be more persistent than non-hybrid parthenogens. Finally, among meiotic parthenogens, parthenogenesis modes under which heterozygosity tends to be lost slowly should be more persistent than modes with a fast rate of heterozygosity loss (see Table 1).

The first prediction is especially amenable to empirical evaluation because there exist many taxa comprising parthenogens with variable ploidy levels (reviewed in Otto and Whitton 2000; Lundmark 2006). For example, there is a great deal of ploidy variation among parthenogenetic species in the worm family Enchytraeidae, and especially among different cytotypes in the species *Lumbricillus lineatus* (e.g., Christensen 1961; Christensen et al. 1989). Extensive ploidy variation has also been characterized in asexual flatworms (*Schmidtea polychroa*; Beukeboom et al. 1996).

Perspective and Conclusions

As discussed above, empirical estimates of age distributions and characterization of patterns of molecular evolution in different parthenogenetic taxa can give insights into

whether sex is often favored in natural populations because it affects linkage disequilibrium, genetic variation, and/or heterozygosity. While the currently available data are insufficient for the comparative studies we are suggesting, research directed at determining the number of independent origins leading to parthenogenesis and the ages of these lineages and estimating rates and patterns of molecular evolution could easily fill these gaps.

Even in the absence of such data, it is interesting to note that several particularly diverse and persistent asexual lineages including the bdelloid rotifers, *Artemia* brine shrimp, and the darwinulid ostracods appear to be mitotic parthenogens (Supplemental Table 1). This may be a coincidental association as mitotic parthenogenesis is the most frequent mode of parthenogenesis in animals. However, an overrepresentation of mitotic parthenogens among the oldest asexual groups may suggest that, for example, that heterozygosity maintenance may be more important to individual- and lineage-level fitness than the production of genetically variable offspring.

There are some important caveats and limitations to our suggested approach. For one, different hypotheses can predict the same patterns. For example, both mutational and heterozygosity-based mechanisms could underlie a pattern where polyploid asexual lineages have higher mean lineage age than diploid lineages. This means that disentangling their relative importance is not always possible. Comparative patterns consistent with some of our predictions could also have alternative explanations than the processes we describe. For example, overrepresentation of higher ploidy levels among old parthenogenetic lineages could instead be a consequence of harboring more targets “capable” of beneficial mutation (Paquin and Adams 1983; Otto and Whitton 2000) or genetic variance that may be beneficial in the face of environmental change (Bell 1982). Older polyploid lineages might also have simply had more opportunities for ploidy elevation (e.g., ploidy elevation via fertilization by males, D’Souza et al. 2004).

To conclude, we believe that comparative studies of parthenogenetic lineages can provide independent lines of evidence for or against the mechanisms likely to play important roles in the maintenance of sex in natural populations, and in some cases, their relative contribution. In particular, the existence of parthenogenetic lineages in many different animal taxa and the wide variation in characteristics such as whether meiosis is involved in reproduction and whether lineages are polyploid or of hybrid origin opens the door to uniquely powerful tests of some key hypothesized advantages for sex.

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