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The delights of understanding what is rare: Why aren’t we all facultatively sexual?

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The delights of understanding what is rare: Why aren't we all facultatively sexual?

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Abstract

Biological diversity abounds in potential study topics. Studies of model systems have their advantages, but reliance on a few well understood cases does not allow to ask why certain phenomena are rare and others common. Rarity itself can provide insight: Darwin realized that the absence of certain taxa from oceanic island can yield information on evolution (via biogeography). Here I focus on facultative sex, which is often hailed as offering the best of both worlds, in that rare sex offers benefits almost equal to obligate sex, and avoids paying most of the demographic costs. It is nevertheless not obviously the most common reproductive mode in nature. I present a model of clonal interference with several options for how sex is triggered, to understand why any 'little sex goes a long way' argument might fail to stabilize facultative sex. One possibility is that nonlinearity selects for sex rates that are high enough that costs erode the adaptive benefits; here the system becomes susceptible to the invasion of full asexuals. I will briefly reflect on conceptual links between social behaviour and sex, and on the need for studies to use demographic and genetic information alike, not forgetting the importance of natural history.

Introduction

I recently had the fortune of lunching with Georgina Mace and other panel members of a grant funding body. In the conversation, she reminded us how lucky we are, working in a field where most researchers are generous and open about their ideas. She reflected on whether the general niceness of a field might be a function of the ratio of the number of 'things' (objects, topics) available to study, and the number of people wanting to study them. The abundance of organisms with diverse life histories, genetic architectures, ecological settings, and idiosyncratic quirks of natural history means that researchers do not need to be particularly anxious of losing their territory to others with similar ideas — and most of us, fortunately, understand this.

This brings about a nice atmosphere (one that may well differ from some other fields of scientific enquiry), but also creates a challenge. The immense diversity of features of biological systems means that all of us have to seek a balance between admiring the idiosyncratic and seeking for generalities in life's messages. One approach is to rely disproportionately on model organisms and tacitly assume that they reflect life as a whole. This approach has its advantages: having in-depth knowledge of *E.coli*, *C. elegans*, *S. cerevisiae*, maize, *Arabidopsis thaliana*, *Ciona intestinalis*, *Chlamydomonas reinhardtii*, *Drosophila*, zebrafish, and *Mus* and *Peromyscus* mice (the list discussed in eLife's recent collection of feature articles on the natural history of model organisms, Alfred and Baldwin 2015) undoubtedly leads to better science that a superficial look at 100,000 species. A highly selective approach to what we study in the tree of life comes, however, with a significant danger of a bias: not all arthropod life obeys *Drosophila* rules e.g. with respect to sexual selection (Zuk et al. 2014). A partial answer may be found in widening the scope of genomic work to encompass more species (Alfred and Baldwin 2015; Russell et al. 2017). This answer is, however, bound to retain a one-sided nature, if not accompanied by equivalently broad efforts to understand the ecology and natural history of each case (Futuyma 1998; Kokko et al. 2017).

There is no top-down control of scientific effort spent across taxa. While I believe that the benefits of a bottom-up approach far outweigh its costs (and the scientific community thus has a duty to defend the freedom of each researcher to choose what to study), this is not to say there is no downside. Individual choices collectively lead to taxonomic chauvinism, the tendency to study species that in some sense are close to humans (Kokko 2017; Troudet et al. 2017). Parallel to this, there are very good reasons to study phenomena (or species) that are common. This is probably a faster route to general messages than focusing on the idiosyncratic and the odd, but a focus on the familiar and on the common does not take full advantage of the general messages that can be found when thinking about rare evolutionary outcomes — or even absent ones. Darwin’s thinking during his voyage on the Beagle was focused not only on what he saw, but also on what he did *not* see: oceanic islands rarely had frogs, even if there was habitat on offer that appeared suitable (Darwin 1859). Such biogeographic patterns are unexpected if species have been created *on site* to match their environment, while a vision of species descending from ancestral forms, with travel difficulties that depend on the species’ traits, explains this with ease. True evolutionary insight can be gained from a lack of examples belonging to a certain category, and Darwin made ample use of this type of insight.

The reasons behind rarity and absence are not always as easy to explain as in the case of oceanic island fauna. Sometimes we have an almost opposite situation at hand: intuition suggest that a pattern of A being common while B is rare could be explained with ease – if only A and B swapped place. This situation arises whenever intuition suggest a very ‘clever’ solution to some adaptive problem and, after having convinced ourselves that it should be common, we find out it to be rare. The particular case I will focus on here is that of sexual reproduction in its facultative mode. Facultative sex is often described as offering most of the advantages of sex (rare sex speeds up adaptation and/or avoids genome decay almost as well as obligate sex, Green and Noakes 1995; Park and Krug 2013; Hojsgaard and Hörandl 2015; Burke and Bonduriansky 2017) while paying very little of the costs (since most generations are asexual and thus demographically efficient). The demographic cost may even itself help speed up adaptation if relatively maladapted individuals are more likely to pay the cost, which can happen under condition-dependent sex (Hadany and Otto 2009). Against this background, if the scientific community only kept studying what is common, we would have missed an opportunity to ask a fundamental question about why life is so often organized the way it is.

Facultative sex: why don’t we all do it?

“Because, simply, facultative parthenogenesis is not stable... it just usually leads to complete parthenogenesis”

— question from the audience after Dr. N. Burke’s talk on sexual conflict and facultative sex
(audio available at: https://programme.europa-organisation.com
/slides/programme_jointCongressEvolBiology2018/webconf/
879_19082018_1140_antigone3_Nathan_Burke_718/index.html)

It took quite some time for evolutionary biologists to realize that sexual reproduction is a mystery because its costs, at least in simple models, appear to exceed the benefits (Williams 1975; Maynard Smith 1976). Complete (obligate) asexuality is known to associate with downsides such as clonal interference (Park and Krug 2013) and the accumulation of deleterious mutations (Hollister et al. 2015) that, taken together, probably can explain the near complete absence of cases where an asexual lineage would have persisted for long and diversified to a great extent (Bell 1982; Ho and Agrawal 2017; Bast et al. 2018, but see also Neiman et al. 2009; Brandt et al. 2017). All this, however, does not explain why the reprodictive mode of *obligate* sex is so common that it is usually taken to be the norm (Green and Noakes 1995; Hurst and Peck 1996; Hartfield 2016; Burke and Bonduriansky 2017), given the advantageous nonlinearities inherent in any version of the "a little sex goes a long way" argument.

One possible answer is that obligate sex only appears common if viewed through our lens of taxonomic chauvinism. Eukaryotic life in general appears to choose facultative sex much more commonly than a focus on large, multicellular animals or plants would suggest (Hastings 1992; Dacks and Roger 1999). When viewed across a broad enough taxonomic lens, sex also does not necessarily associate with the production of males. Sexual conflict, where males benefit from mating while females might not, can complicate the maintenance of facultative sex (Gerber and Kokko 2016; Burke and Bonduriansky 2017), but this argument only applies to species with males (anisogamy).

Another possible answer is more subtle. If sex brings about benefits that relate to enhanced efficacy of selection, benefits will occur at the lineage level but cannot be easily assigned to the individual performing the sexual cycle (Burt 2000). A situation arises where the costs are paid immediately, but the benefits accrue over longer term; this makes a facultative sexual population vulnerable to invasion by mutants that engage in sexual reproduction less often. Therefore, obligate sex might prevail not because it is fundamentally able to resist asexual mutants, but because it represents a more robust system than facultative sex when it comes to the production of competing reproductive modes. In other words, transitioning from obligate sex to facultative sex or asex is hard (Engelstädter 2008; Bengtsson 2009; Neiman et al. 2014), while microevolutionary changes in the rate of sex happen much more easily (Roze 2014). Indeed, evolutionary responses in the rate of sex are frequently reported in experimental evolution approaches (e.g. Becks and Agrawal 2010, 2013; Luijckx et al. 2017).

Although rates of sex are not usually discussed using evolutionary terminology of cooperation and conflict, one could consider doing so: sex is then interpretable as a way to produce a public good (Frank 2010) of a higher rate of adaptation, produced by individuals who engage in costly acts. A ‘cheater’, then, is a genotype with a lower rate of sex. Viewed in this light, Burt’s (2000; see also Bengtsson and Ceplitis 2000) argument that facultative sex is only stable in the presence of clear ecological differences between sex and asex (e.g. dormant offspring that are produced sexually) can be translated as there being constraints that prevent cheating from spreading to fixation.

Below, I will reflect on the extent to which this viewpoint holds. I will present a model that shows several unresolved questions regarding the stability of facultative sex, including an underappreciated possibility, which represents a mirror image of the prediction of rare-sex cheaters spreading as they overexploit the public good. In this alternative, the rate of sex evolves upwards (sexuality offers a sufficient short-term advantage) if it is initially low. But if the advantage gained through sex is always less than what is required to overcome a twofold cost should such a cost be paid in every generation, there must exist a rate of sex after which the demographic costs become prohibitive, and the system stabilizes at an intermediate sex rate (see Roze 2014 for a similar analysis up to this point). But the system's stability must also be contrasted with the success of asexuals or obligate sexuals invading. Although it is difficult to express the stochastically accruing adaptive benefits and the relatively deterministically paid demographic costs in the same currency (see below), the results suggest that the 'net benefit' of sex has, upon stabilization of the rate of sex, been eroded to the extent that the population has become vulnerable to invasion by asexual mutants.

The gap between genetics and ecology: on the difficulty of measuring the pros and the cons

Published models vary significantly in their focus on the genetic or the demographic aspects of sex. This is understandable: science progresses as a series of publications, each of them being of finite length, and necessarily trying to solve one piece of the puzzle at a time. Reviews, too, need to define their angle such as disentangling various costs of sex (Lehtonen et al. 2012), facultative sex when there is conflict between males and females (Burke and Bonduriansky 2017), or whether a call for a pluralistic understanding of sex (West et al. 1999) has been followed since its publication (Neiman et al. 2017) — rather than try to cover a vast field in its entirety. It is intriguing to note that key monographs on the evolution of sex were published some decades ago (Williams 1975; Maynard Smith 1976; Bell 1982), with apparently no equivalent effort being undertaken today.

Similar specialization applies to models published today. One category of models briefly mentions that sex is costly (the demographic aspect) while focusing on the genetic consequences (the intriguingly titled *What's wrong with a little sex?* by Peck and Waxman

2000 is an example of this approach, worth a specific mention as they provide an alternative route to less sex — based on heterozygote advantage — complementing Burt's 2000 argument). Often, a model of this kind asks whether the proposed mechanism might be sufficient to overcome a twofold cost. Another category of models leaves the genetic side largely aside and ask exactly how costs play out in complicated demographic scenarios (reviews of such models: Lehtonen et al. 2012; Meirmans et al. 2012; a more recent example: Stelzer and Lehtonen 2016).

A better unification of these two approaches seems timely, for otherwise statements that enthuse about the ability of facultative sex to combine the advantages of both sex and asex (D'Souza and Michiels 2010; Kleiman and Hadany 2015; Burke and Bonduriansky 2017; Gerber et al. 2018) remain without quantitative support. The usual approach, that many facultative sex models adopt (e.g. Hadany and Otto 2007, 2009; Roze and Otto 2012; Roze 2014), is that individuals allocate some fraction of their reproductive effort to sexual reproduction each generation; the cost paid is linearly related to this fraction. While this is an adequate approach when the production of sexual offspring does not vary over time, a simple thought experiment is sufficient to illustrate that nonlinearities arise if sexual generations occur in synchrony, and asexuality prevails in between.

Consider a highly simplified situation where facultative sex brings about a fitness advantage of magnitude s, such that every individual in this lineage has relative fitness $1+s$ compared with an asexual individual's fitness 1; this is halved, due to a twofold cost of sex, in all generations where the facultative sexual lineage uses its sexual cycle (taking into account the cost, the lineage's contribution to the next generation is now $(1+s)/2$). If sex occurs once every 10 generations, is the twofold cost reduced to 1/10th of its original value (1.1-fold cost instead of 2-fold)? This answer would be wrong. To make a cost of sex statement precise, it is best expressed by computing the *s* that brings the sexuals' fitness up to the same level as the asexual when viewed over multiple generations (Lehtonen et al. 2012); any *s* higher than this, and the sexual lineage will outcompete the asexuals. Since generations follow each other with fitness behaving multiplicatively, the correct way to deal with temporal variation in fitness is to use the geometric mean (Starrfelt and Kokko 2012), and solving for $((1+s)/2 \times (1+s)^9)^{1/10} = 1$ yields the solution $s = 0.0718$, thus the cost is a 1.07-fold one. Note that the geometric mean is often usefully expressed with logarithms, in this case $e^{(\ln((1+s)/2)+9 \ln(1+s))}$, which gives the same answer but would in lengthier computations be less susceptible to rounding errors.

Should the fitness advantage *s* enjoyed by the facultatively sexual lineage also experience temporal variation, the situation becomes more complicated again. One can still quantify which lineage is expected to take over: for example, consider a setting where the *s* of the facultative sexuals is, immediately following sex, nearly twice as high as the 0.0718 above (obtained by setting $s_1 = 0.14$ where 1 denotes the first post-sex generation), but this advantage erodes over time when the lineage multiplies asexually is employed, and as soon (at generation 10) when it drops to the level of the obligate asexuals, the population performs a twofold-costly sexual cycle. Assume, for a simple numerical example, a sequence of s_i values {0.14, 0.12, 0.10, 0.08, 0.06, 0.04, 0.03, 0.02, 0.01, 0}, the last value interpreted as no benefit s_{10} left at the point in time when the population reproduces sexually and the demographic cost is paid such that the population is halved in this generation. The geometric mean fitness is

$$e^{\ln(1.14)+\ln(1.12)+\ln(1.10)+\ln(1.08)+\ln(1.06)+\ln(1.04)+\ln(1.03)+\ln(1.02)+\ln(1/2))} = 0.8785$$

which clearly falls below the 1 which we assumed to apply to the asexuals. Note that if we had simply taken an expectation based on the arithmetic mean of the demographic performance of the population, we would have gained an incorrect answer of 1.009. This entirely hypothetical toy model can be criticized on many grounds — e.g. it is implausible that the reference asexual population keeps its fitness at 1 throughout, given that asexuality in the facultative sexuals erodes fitness so quickly — but its aim is to simply highlight a key point: variance in the demographic performance of a population has an impact on its ability to outcompete alternative reproductive modes, and facultative sex might be particularly prone to experiencing such fluctuations.

It is interesting in this regard that we know much more about the population genetic and genomic consequences of rare sex when employed by all members of a population (Roze 2014; Hartfield 2016, 2018) than how it behaves when competing with alternative reproductive modes. If facultativeness coexists, even temporarily, with obligate sexuals, gene flow will occur between the two modes (Hadany and Beker 2007; Kleinman and Hadany 2015). Even asexuality is not always a guarantee that reproductively isolated populations will form, as anisogamy can create special cases where asexuals have some access to sex via males. This possibility arises because, for a given female, not mating with a male does not logically preclude males being produced by that same female. Details depend on the system, but thelotokous asexuality can spread this way in the haplodiploid wasp *Lysiphlebus fabarum* (Sandrock and Vorburger 2011), and *Daphnia* males are produced by mothers without fertilization, allowing them to become vectors of contagious asexuality (*Daphnia pulex*, Paland et al. 2005). In general, if parthenogenetic females still produce males, or if parthenogenesis in a hermaphrodite only applies to the female function (Mogie

2011), then alleles for parthenogenesis can spread via siring activities of males from the asexual lineage.

In the following, I will show how a relatively simple spatial model, based on a single well studied benefit of sex (clonal interference), can yield insights and further questions that would not be achievable if keeping the focus on only the invasion prospects of radically different reproductive modes against each other, or on the modification of the rate of sex. While considering these in parallel, I also consider several scenarios regarding how exactly an organism chooses to use facultative sex.

Modelling facultative sex when both asexuality or obligate sexuality is an option

There are many mechanisms available to introduce a potential benefit of sex into a model (Hartfield and Keightley 2012; Roze 2012). I base my model on that of Kim and Orr (2005), who considered the faster rate of evolution in a sexual vs. asexual population when a modest number of sites can mutate to a beneficial version. In a finite population with a sufficient mutation rate, lineages with different beneficial mutations compete in asexuals (clonal interference), and can therefore fix faster in sexuals as each mutation does not have to arise in a genome that already contains the other (Fisher-Muller effect, Fisher 1930; Muller 1932). My choice is based on the empirical support that has recently accrued for a role of clonal interference in the evolution of sex (Colegrave 2002; McDonald et al. 2016) as well as the relatively well understood nature of this process (Park and Krug 2013). Here, ‘relatively’ refers to the fact that, to my knowlegde, we have a well developed theory on the effects of rate of sex when the entire population follows this rate (Hartfield 2016, 2018), but no analytical picture of what happens when facultative sexuals exist with gene flow to and from obligate sexuals, or when different rates of sex compete in the same population.

I present simulation results to be able to fully account for the complexities of competition of two or more genotypes, together with the temporal dynamics involved in the cost of sex as explained above.

Genotypes

The reproductive mode of each individual is determined by one diploid locus with (up to) three alleles: a (asex), f (facultative sex), and o (obligate sex). For dominance relationships, I assume that af and ao individuals are asexual, and fo sexuals are obligately sexual. In a subset of simulations, I let two different facultative sex rates f_1 and f_2 compete, in which case a heterozygote (f_1f_2) is assumed to use the higher of the two rates as its reproductive mode.

The *n* other diploid loci determine fitness components other than the cost of sex, and they are all initialized with a wildtype allele 0. They mutate (rate μ) to a beneficial allele, with no back mutation. Each beneficial allele is dominant and brings about a multiplicative fitness benefit of magnitude *s* (i.e. no epistasis). Thus, with $n = 10$ loci (the value of *n* used in the examples of all the figures), the maximum fitness achievable by any individual is $(1+s)^{10}$. Each simulation is stopped when the first individual arises that has this fitness value, as thereafter, for a subset of the population, no further adaptation is possible. As my goal is not to track time to fixation but to see when each reproductive mode can outcompete the others, I also stop the simulation if one mode — i.e. a certain rate of sex (including obligateness), or asex — is expressed by 100% of the individuals.

Competition

I use a spatial setting with up to 3 subpopulations to be able to track, in a single simulation run, the prospects of invasion of any of the participating reproductive modes by each other

(Figure 1). Each subpopulation has *N* individuals such that the global population equals 3*N* if all three subpopulations compete, and 2*N* in pairwise competition contests. (My main figures are based on $N = 3333$, bringing the global population as close to 10^4 as possible while being divisible by 3). Each generation consists of local reproduction (see below) followed by an exchange of migrants, where one migrant per generation follows each arrow in Figure 1. Note that the colours on the arrows strictly only apply to the first generation, where each subpopulation is initialized with homozygotes of the respective reproductive mode. If, subsequently, a reproductive mode spreads in a population different from its original one, representatives of this mode can also be chosen as migrants (I assume no genotypic differences in the propensity to migrate; see Discussion for dispersal in facultative sexuals).

The first step of reproduction is to determine which individuals engage in sex in the current generation. For asexuals and obligate sexuals, the answer is clear. For facultative sexuals, there are far more choices of the rules that determine when precisely they engage in sex, and this is likely to matter. If they do so in asynchrony with each other, sex will proportionally more often make them tap into the gene pool of obligate sexuals (assuming they exist) than if all facultative sexuals mate simultaneously in the same generation. Environmental triggers of facultative sex can also co-occur with sex being condition-dependent (Mostowy and Engelstädter 2012; Griffiths and Bonser 2013; Ram and Hadany 2016). If we assume that organisms can sense their relative performance in the local population (e.g. through competitive resource accumulation where less well adapted individuals fall behind), then theory suggests relatively good prospects for condition-dependent sex via an ‘abandon-ship’ mechanism. There is a potential problem: if facultative sexuals mate in synchrony (based on the environmental trigger), they largely mate with others who also are relatively maladapted, and their access to the better-adapted part of the gene pool might remain compromised, at least relative to what is assumed by published models where, in every generation, a nonzero fraction of facultative sexuals, or a fraction of each facultative individual’s reproductive effort, utilizes sex (Hadany and Beker 2007; Hadany and Otto 2007, 2009).

Finally, so far I have avoided assuming that there is a male and a female role in reproduction: egg and sperm production are not roles typically found in sex in unicellular eukaryotes. Facultative sex can, however, also occur in gonochores (dioecious organisms) or in hermaphrodites. These are systems where males exist, opening up unusual possibilities such as contagious asexuality (e.g. Paland et al. 2005; Sandrock and Vorburger 2011) that can arise because males (or the male function of a hermaphrodite) do not have to stop reproducing sexually even if they carry alleles that make females (or the female function) parthenogenetic. I here ignore male production in gonochores due to the the very complicated timing issues that arise when not all female reproduction requires males (Aparici et al. 1998; Halkett et al. 2004; Gerber et al. 2018), and I will instead investigate contagious asexuality in a hermaphroditic case where the male function exists whether or not the lineage is sexual. In other words, if an organism abandons sex either in the current generation or completely, in the sense of becoming parthenogenetic via its female function, it may or may not also shut off its male function. Parthenogenetic lineages may therefore ‘infect’ sexuals and turn their offspring into parthenogens.

To accommodate the above considerations, I consider four different scenarios for the features of the facultative sexual lineage:

A. Asynchrony. The rate of sex is the probability, applied independently to each facultative sexual, that the individual performs a sexual cycle in the current generation.

B. Synchrony. In each generation, a uniformly distributed random number is drawn (identical for the entire global population), and if it falls below the rate of sex, all individuals who obey this rate perform a sexual cycle. The random number corresponds to an environmental trigger that is perceived by all members of the facultative sexual population. Note that in cases with two rates competing, a strong enough trigger (low enough value of the random number) means that all facultative sexuals have sex, while a somewhat less strong trigger means that only those with a higher rate of sex do.

C. Condition-dependent sex. Like assumption structure B here, but with an additional criterion: for the facultative sexual to engage in a sexual cycle, the number of loci at which it harbours at least one beneficial allele must fall below the median of this measure for all members of its local population. Note that the realized rate of sex, averaged over all facultative sexuals, now has the environmental trigger frequency as its upper limit (the realized rate will be close to this limit if facultative sexuals adapt more slowly than the mode they are competing against, and clearly lower if they adapt faster).

D. A hermaphroditic life cycle that permits contagious asexuality. Each individual (of any reproductive mode) has a male and a female function. The rules for facultative sexuals are identical to scenario B, but this is applied to the female function only. The sire will be chosen randomly among any individual in the local subpopulation, regardless of its reproductive mode.

In each case, each subpopulation produces *N* offspring (after which the parents die). The 'mothers' of each offspring are chosen first, and the 'sire' is then assigned next. I use these terms in quotes to remind the reader the use of sex-specific language should not prevent us from noticing that one individual can function in either role (none of the cases A-D are gonochoristic); the 'mother' is simply the individual whose reproductive mode determines whether another individual (the 'sire') is needed or not.

Each individual's propensity to be chosen as the mother is

$$p_i = \begin{cases} (1+s)^{k_i} & \text{if currently asexual} \\ (1-c)(1+s)^{k_i} & \text{if currently sexual} \end{cases}$$

Here *c* is the cost of sex (0 ≤ *c* ≤ 1, though in practice an upper limit of 0.5 is relevant if one wishes to model costs up to twofoldness i.e. the halving of demographic output), k_i is the number of loci at which individual *i* has at least one beneficial allele, and 'currently asexual or sexual' reflects the phenotypic choice made by the individual in the current generation regarding its reproductive mode. Note that the model ignores any permanent costs of facultative sexuality that would have to be paid in asexual generations (i.e. costs of phenotypic plasticity, Auld et al. 2010).

The 'sires' are thereafter chosen for those offspring whose mothers are currently sexual. In scenarios A to C, the sire is chosen among all sexual individuals, with propensities

$$q_i = (1+s)^{k_i}$$

Note that the cost of sex is irrelevant in this expression, as all potential sires are sexual and compete with each other. In scenario D, the expression for the q_i is the same, but now every individual in the local population has a nonzero propensity, not just the currently sexual ones.

Propensities translate to actual parentage in a probabilistic manner, e.g., if a population only had three potential sires, one with propensity 1.0, another with 1.01 and a third one with 1.0201 (the outcomes for no, 1 or 2 beneficial alleles if $s = 0.01$), the first individual is chosen with probability 1/3.0301, the second with probability 1.01/3.0301, and the third with probability 1.0201/3.0301. Migration then follows with each subpopulation exchanging one randomly chosen migrant offspring, and a new generation ensues.

Results

I follow a computational variant of Kreyling et al.'s (2018) argument, that potentially nonlinear responses are more usefully studied using a fine-scaled mesh of alternative parameter values and representing each outcome with little or no replication, than to focus on few extensively replicated locations in the potential parameter space.

I therefore present two types of figures to depict the outcomes. First (Figs. 2 and S1), the global population composition is depicted, at each parameter value (x axis: the rate of sex used by facultative sexuals, y axis: cost of sex c), as a miniature map with two or three bars depicting the two or three subpopulations present in the simulation, and the relative frequency of each reproductive mode at the end of the simulation indicated within each bar with colours that match Fig. 1A. Thus, if none of the three modes was able to invade any other, the pattern equivalent to the Belgian national flag emerges (black to the left, followed by yellow, then red; Fig. 2A, middle column, contains several examples). If facultative sex invades all of the asexual subpopulation and half of the sexuals, then most of the small map is yellow, with a ½-height red bar still visible in the rightmost population; other competitive outcomes follow a similar logic. These maps are modified to have only 2 bars in cases where only two reproductive modes competed against each other.

Second, I also investigate the direction in which a facultative rate of sex evolves (towards more frequent or less frequent sex). Here I use two populations initialized with different rates of sex, one with f_1f_1 homozygotes, another with f_2f_2 homozygotes. A green arrow to the right (Fig. 3, Fig. S2) indicates that the higher sex rate spread at the expense of the lower sex rate (at the end of the simulation more than N of the $2N$ individuals use the higher rate) in at least 2 of the 3 simulations; a large arrowhead additionally indicates that all of the 3 simulations agreed on the outcome. If the lower sex rate won, this is correspondingly indicated with blue arrows pointing to the left.

The scenarios A-D clearly differed from each other, with D (contagious asexuality) following fundamentally different dynamics from the rest (Figures 2, 3), and A-C showing more subtle differences. I therefore discuss the patterns A, B and C first. For all these cases, at very low costs of sex, obligate sex becomes a serious competitor of facultative sex, and perhaps surprisingly, obligate sex is best able to displace facultative sex when the latter uses a very low rate of sex. This is surprising if focusing on the costs (at this end of the parameter spectrum, the demographic ‘savings’ of facultative sex are at their largest), while perhaps predicted if focusing on the benefits (facultative sexuals might fall behind significantly if they only very occasionally engage in sex). The pattern of obligate sex vs. facultative sex, as a whole, shows nonlinearities, with the very lowest rates of sex and the very highest rates of sex being less favourable to facultative sex than low-intermediate rates.

Asexuals, on the other hand, can outcompete facultative sex when the latter uses sex frequently and when the cost of sex is high (top right corner in scenarios A, B, Fig. 2). This pattern is clearly driven by the demographic cost of sex being at its highest. Asexuals can also, much more stochastically, replace facultative sex when the sex rate is low. At low sex rates, facultative sexuals behave like asexuals in most generations, and when each parameter setting is only replicated once, the role of genetic drift becomes easily visible. Each migrant (that forms the invasion pressure to neighbouring populations) is chosen without respect to genotype. Therefore, migrants' reproductive mode is only linked to their adaptedness (measured as k_i) if sex allows the local population to accumulate beneficial mutations faster than its asexual neighbour. If the rate of sex is too low to create a clear difference, drift can become an overwhelming determinant of the reproductive mode that prevails (except, in the setting where all three reproductive modes compete, obligate sex will determinitically disappear at high costs of sex). Significantly larger population sizes (N = 50000, with 15 migrants per generation) have only a limited effect changing the fundamentally stochastic pattern at low rates of sex (Fig. S3).

Turning to the differences between A, B and C highlights that different ways of triggering facultative sex can matter for the outcome. There is relatively speaking 'more yellow than red' in A than in B, indicating that asynchronous facultative sex indeed can be of benefit when sex evolves to alleviate clonal interference, and when there is (at least initially) an obligately sexual lineage present whose beneficial alleles can be acquired by having sex facultatively. In those cases, facultative sex can sometimes fix, but the question then remains if the rate of sex (fixed within each setting of Fig. 2) is stable (Fig. 3 as discussed below). I will return, in the Discussion, to the question of why facultative sex in reality often is synchronous, if the current results indicate a (subtle) benefit to it being asynchronous.

In scenario C, the stochastic outcome dominates the entire large-cost region; there is no clear threshold for the combination of a cost and rate of sex above which asexuality is guaranteed to win. One possible interpretation is that condition-dependent sex is better able to resist asexuality because of its intrinsic superiority (‘only pay for sex when you really need it’ appears smart). However, note also that by definition, only a subset of the facultative sexual population responds to the environmental trigger that calls for sex at a rate as indicated on the x axis, and the rarity of realized sex may simply shift all or most parameter values into a region where drift is the main determinant of competition between reproductive modes. This interpretation however fails when also considering Fig. 3: high rates of sex show a more deterministic outcome than low rates of sex.

Finally, case D differs starkly from all the others. Here, asexuality, via a contagious process, clearly establishes itself, except that it can fail to do so when the sex rate is low (which makes the contagion process work poorly). In case D, being ‘contagious’ applies not only to asexuals but also to currently asexual facultative asexuals; thus if asexuality is not permitted as an option (rightmost graphs, Fig. 2), then obligate sex is never able to resist the invasion of facultative sex. Here, effectively, the cost of sex is significantly lowered for the facultative sexuals: their female function only rarely pays this cost, while I assumed no demographic penalty (relative to obligate sexuals) when acting as males.

Given the amount of yellow (facultative sex) in Fig. 2, is facultative sex then stable or not? Pairwise or 3-wise competition scenarios (Fig. 2) do not answer whether shifts in the rate of sex within the reproductive mode of facultative sex might lead a population towards a zone where it becomes invadable by another mode. Turning to pairwise competition scenarios of an initial f_1f_1 population that exchanges migrants with an f_2f_2 population reveals, again, a role for drift: not all simulations agree on which rate of sex wins (Fig. 3). This is to be expected especially at low rates, as the two competing rates are phenotypically indistinguishable in most generations.

The role of stochasticity is diminished at higher rates of sex (Fig. 3). Here, the patterns clearly mirror those of Fig. 2. Within areas where asexuality, if it was an option (Fig. 2), was able to deterministically outcompete facultative sex, rate of sex contests (Fig. 3) favour lowering the rate of sex. Remarkably, just below the threshold rate of sex from which onwards asexuality begins to win (Fig. 2), facultative sex is selected to occur at a higher rate (green right-pointing arrows, Fig. 3).

This supports the hypothesis that there is selection to use sex ever more often until its costs have increased to erode the entire net benefit relative to an asexual lineage. At this point, a facultative lineage becomes vulnerable to asex, not via evolving an ever lower rate of sex, but by having damaged its own demographic performance via costs of sex that effectively negate the beneficial effects on adaptation. Notably, this threshold was not reached by condition-dependent sex (Fig. 3C), which instead was able to reach a systematically high rate (but one that is not, by definition in this case, used by all the members of the population).

Discussion

To follow the gist of the symposium, I will discuss both the scientific lessons from the exercise above, and end with some general hopes for the future.

Regarding facultative sex, there are two main messages. First, facultative sex is rare, and it is a valid question to ask whether there is something systematic that prevents it from being stable (except when additional forces, such as being coupled with dormancy or dispersal, come into play, Burt 2000). The model shows that the statement ‘significant benefits accrue already at low rates of sex which allows costs to be paid rarely’ is crucial for understanding the fate of rare sex. Importantly, however, tempting potential corollaries of the form (i) ‘hence, low rates of sex should be stable’, (ii) ‘hence, facultative sex is unstable because it is vulnerable to cheats who use sex ever less often’, or (iii) ‘hence, facultative sex is unstable because sex rates might increase until obligate sex emerges’ are not self-evidently true (even though some may arise in some models — e.g. if asexuality is *not* considered as an option, then obligate sex can sometimes outcompete facultative sex, Hadany and Beker 2007; my model remains more cautious regarding obligateness’ success, even if setting benefits to very high values, Fig. S1-S2). A predominant – and still not universal – pattern in my model was that higher rates of sex evolved (to help alleviate clonal interference) together with the associated demographic costs increasing, until a point was reached where the reproductive mode, due to its demographic disadvantage, is no longer able to resist invasion by asexuals.

Second, while the ‘eroding net benefits’ case is perhaps the most thought provoking outcome of the model, it is not the only one. The cases I modelled are a small subset of what is possible with respect to the demographic rules that a facultative sexual might follow. For example, the availability of males in organisms with separate sexes brings about a whole new set of choices — who produces the males, how long they are available for females, and can they force a female to fertilize her eggs should she prefer to remain asexual, Gerber and Kokko 2014; Burke and Bonduriansky 2017; Gerber et al. 2018). Even so, the outcomes were different for each scenario, with sometimes drastic (in the case of contagious asexuality) and sometimes milder consequences.

One has to warn against using the global amount of facultative sex in the model output (amount of ‘yellow’ in Fig. 2) to predict, across scenarios, where we should find facultative sex in nature. This is because the ability of facultativeness (of a given rate) to outcompete asexuals and sexuals does not yet prove stability against lower or higher rates of sex. If these can evolve, the population may shift towards a region of vulnerability with respect to another reproductive mode invading. In other words, the Achilles’ heel of facultative sex is that plastic or microevolutionary adjustments in sex rate can occur irrespectively of whether this increases or decreases the prospects of a 0% or 100% sexual lineage invading. With this in mind, it is worth considering some details.

The first intriguing detail is that condition-dependent facultative sex (scenario C) appeared not to suffer as greatly from asexual invasion as the other scenarios, in which facultative sex occurred irrespective of condition. This fits with the general gist of the finite but significant literature where facultative sex performs well if it utilizes the abandon-ship mechanism (Hadany and Otto 2007, 2009; Schoustra et al. 2010; Mostowy & Engelstädter 2012). A more skeptical look at Figs. 2-3, however, reveals a difficulty of matching the varying (potentially low) rates of condition-dependent sex with the guaranteed rates that the x axis values in the other scenarios refer to. However, not all all of scenario C in Figs. 2-3 is in the ‘drift’ region where sex is so rare that asexuals and facultative sexuals perform similarly: there is clearly a difference between the left and the right end in directionality of selection in Fig. 3D. Biologically, too, the advantageous nature of condition-dependent sex appears to hold: if an allele promoting sex often resides in individuals that, by virtue of being in good condition, shield the allele from expressing the demographic costs of sex, we can expect a much better cost-benefit balance than if all individuals obeyed the environmental trigger without inspecting the status of self. It is interesting that this thrifty approach to cost appears to override an obvious downside of condition-dependent sex: matings do not allow access to the best adapted part of the gene pool.

Earlier work in a different setting (Hadany and Otto 2007) similarly showed that condition-dependent sex can spread despite not having access to the very best genotypes. Note also that the entire problem of access might disappear in some formulations of condition-dependent sex, which have not been modelled by myself or (to my knowledge) by anyone else. If condition-dependence (my scenario C) combines with facultativeness in only the female part of hermaphrodites (my scenario D), or only females of a gonochorist, then the life history will restore access to well adapted genomes. Such sires might even disproportionately contribute if well adapted, in case of significant sexual selection (Hadany and Beker 2007; Roze and Otto 2012; note however that the rate of sex was not condition-dependent in these models).

Another intriguing result is that synchronous facultative sex appeared somewhat less able to outcompete obligate sex than asynchronous facultative sex. In nature, facultative sex is often expressed under stressful conditions (Nedelcu and Michod 2003; Abe et al. 2005; Griffiths and Bonser 2013), causing synchrony. I believe this discrepancy is not a difficult one to explain, though it requires admitting that my model (like any) does not capture all there is to mating in real systems. Asynchrony removes most of facultative sexuals as potential mates (assuming rates of sex less than ½). This situation can be beneficial to an allele coding for facultative sex as long as facultative sexuals coexist with obligate sexuals, as the latter are predicted to have the highest rate of adaptation. Better access to beneficial alleles from obligate sexuals is especially significant if sex is rare and drift removes variation within facultative sex lineages. If facultative sex is has fixed (note that my simulations did not proceed beyond this point), access to obligate sexuals as mates becomes irrelevant, and another problem arises: an asynchronously sexual population may offer very few potential mates. My model did not include any form of mate limitation as a demographic problem (in the extreme case, if a subpopulation had only 1 sexual individual, the rules for the choice of parents lead to the 'mother' being identical to the 'sire', i.e. selfing was allowed). In reality, the reliance on an environmental trigger might bring about mate-finding benefits of synchrony, but it remains an open question how this might interact with condition-dependence. Perfect synchrony with an unanimous response to environmental triggers leaves little room for condition-dependent reaction norms to operate.

A final contrast between model output and the occurrence of facultative sex in nature is that the model has difficulty producing facultative sex as the reliably winning outcome at low sex rates. Larger population sizes could, in principle, help to achieve a more deterministic outcome (Park and Krug 2013), but if sexual events remain scarcely distributed in time, increasing N does not by itself remove the role of chance as a determinant of whether facultative sexuals with rare sex win over asexuals (Fig. S3). Microbial populations often feature rare sex as well as large effective population sizes (though it is probably premature to say if the rate of sex covaries with N_e, see Constable and Kokko 2018). On the other hand, ininsects, large population size appears to covary with asexuality (Ross et al. 2013). Further work on the stability of rare sex at large N_e would be welcome.

Obviously, like with any modelling exercise, I have created an assumption structure that leaves aside potential alternative choices with respect to, e.g., the genetic structure employed (my approach only focused on one of the many processes suggested to select for sex), the parameter values (see Fig. S1-3 for some alternatives), and the way the reproductive modes compete. The spatial competitive setting has its advantages as it can summarize two-way or three-way invasions at once, and the parameter mosaics thus created allow flexible interpretations. One can argue, for instance, that movement along the arrows in Fig. 3 occurs readily, and if the emergence of an asexual type is allowed to occur (attention now moving to Fig. 2), it should do so in the zone (rate of sex) where the facultative sexuals have stabilized (the location defined by Fig. 3 with the tips of green arrows meeting those of the blue). Although mutations between reproductive modes were not included, I believe that the migration process (e.g. between asexual and a type of sexual) also captures the gist of a mutant asexual arising from among the sexuals, because simulations in Fig. 2 were started independently from the outcome of Fig. 3, with every individual at the beginning of the adaptive road ahead. However, my approach may favour the sexual modes more than a pure mutational approach (from sex to asex) would in subsequent generations, as I do not allow new asexuals to arise from within sexuals that have already adapted for a number of generations.

To return to the big question: why is a ‘best of the both worlds’ strategy rare in nature, at least in the sense of one of its competitors, obligate sex, being employed by large metazoans rather frequently? One potential answer was provided by the model above: if asexuals and obligate sexuals are not currently competing with facultative sexuals, selection will operate on rates of sex without any attention being paid to whether the population is pushed to a boundary of a parameter region where benefits of sex still outweigh the costs. From this boundary onwards, vulnerability to asexual takeovers can happen. However, this is a partial answer at best, not only because of model specifics (other models highlight alternative routes to zero sex, e.g. Roze and Otto 2012), but also because condition-dependent facultativeness appears to avoid many of the problems of condition-independent sex. Also, the summary above does not explain why asexuality does not equally easily invade obligate sexuality. Obligateness, after all, comes with the maximal costs (paid every generation) without any clear improvement of the benefits.

Here, interpreting the model requires additional insight from other published work. Obligate sex can be stable in the model against both asex and facultative sex, but only if the costs are kept low (and when one remembers an important caveat — its stability was only tested against one facultative sex rate at a time). This yields some indirect support for the idea that obligateness can only have evolved under low-cost conditions (Lehtonen et al. 2016), where it can potentially fix. Constraints may then accumulate that make the subseqent invasion of asexuals relatively difficult (Engelstädter 2008; Lehtonen et al. 2016). If anisogamy thereafter arises, the cost of sex shoots up, but this is largely irrelevant for the fate of obligate sexuals that may have lost the machinery to perform asexual cycles efficiently; the cost change does not imply a ready supply of fit asexuals. Being ‘stuck’ with males then also makes the population stuck with the benefits of sex, which include long-term diversification of obligately sexual lineages. Preventing the flexibility that variable sex rates offer is, in this scenario, more a blessing than a curse.

This brings me, finally, to the more general messages. Pluralistic views on sex have been expressed before (West et al. 1999; Neiman et al. 2014 and references therein), and in general, it is difficult to avoid talking about constraints when discussing why all life has not chosen options that our models, or intuition, suggests are the superior ones. The problem of resorting to constraints is that it is difficult to prove causalities. The obligate sex question might benefit from being looked at through the lens of genetic or genomic architecture (Blows and Hoffmann 2005; Mank 2017), regulatory networks (Payne and Wagner 2018), dynamical features of eco-evolutionary feedback loops (Cotto 2017) or any of the many alternative approaches that have been used to study constraints in general — yet the problem remains that much of the action happened so far in the past, and as highlighted many times, the question of the origin of sex is not equivalent to its maintenance (Lenski 1999; Lehtonen et al. 2016). Still, if quite a simple model was able to produce novel predictions as soon as competition between different rates of sex, the invasion of different modes of reproduction, and various demographic scenarios were combined in the same framework, there is clearly more work to be done looking at current invasion prospects of alternative modes.

A firm knowledge of natural history also appears necessary (Futuyma 1998). In the case of facultative sex, sexuality very often associates with the formation of survival structures (e.g. dormancy) and/or dispersal (Gerber and Kokko 2018). While I did not allow this to play a role in the current model, the study of this association appears particularly relevant to condition-dependent sex. The heuristic idea is that asexuality is a strategy with a mindset of “don’t fix it if it ain’t broken”: the genotype of the parent is assumed to be a sufficently good template for all future generations too. Philopatry (as opposed to dispersal) and direct development (as opposed to dormancy) are, in this heuristic, alternative manifestations of this same optimism: drastic changes along any spatial or temporal axes are unnecessary if the here and now are perfectly good. When the rationale behind optimism begins to crumble — e.g. avoiding dispersal will not work for all offspring for the simple reason that the locality becomes crowded (Hamilton and May 1977) — it is easy to see why some diversification is expected with respect to time (dormancy), spatial location (dispersal), and perhaps also ‘identity’ (genetic background for an allele that induces sexual reproduction), even if each of the means of diversification carries some cost. What is harder to see is why an organism would pay several costs simultaneously to achieve the same outcome, and work in this area is truly in its infancy (Gerber and Kokko 2018 produce one model, but as always with a single model only, the modelling choices made regarding e.g. the adaptive process are just one option out of many).

As a whole, there probably is no better remedy for the problems I've highlighted than to talk to each other more. To come back to the Georgina Mace quote: it is wonderful that there's so many things we can study. The flipside of the danger is that each 'thing' — be it a population genetic approach, cataloguing the natural history of lots of organism, an in-depth study of one model organism, a detailed demographic analysis of another — offers so much wondrous detail that few of us dare to do what Williams (1975) or Maynard Smith (1976) did, commenting on the big picture in one go. I also believe that their multi-interested personalities could be usefully resurrected in today's players. Remarkably, both authors commented extensively on the evolution of cooperation in their other writings. I will therefore state one crossdisciplinary big-picture question for the end: does the model above show that (facultative) sex falls victim to the so-called Tragedy of the Commons (Rankin et al. 2007), in the sense of 'selfishness' winning and leading to the erosion of the benefit of better adaptation? I began working on this project expecting the metaphor to work, but it only did so to a degree, in the sense that facultative sex, where it stabilized, failed to do so in a rate of sex region that would have provided an ability to resist an alternative mode of reproduction (even if such rates existed in the model and could have been stayed at). The erosion did not happen via a route of ever-rarer sex, where selfish cheaters would have occasionally tapped into the gene pool of those who do the (demographically) hard work of adapting via sex. Although the metaphor might ultimately prove of limited value (especially if sex is condition-dependent, for the 'cheaters' then pay more of the cost, Hadany and Otto

2009), I do not believe the alternative routes to asex have been pitted against each other explicitly before, and while I failed to produce these results in time for Evolution 2018, I hope they're equally interesting now in 2019 [which is when I imagine the special issue to be published].

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Figure legends

Figure 1. A. The basic setup of the competition, when all three subpopulations are allowed to compete. In alternative setups, one of the three subpopulations is absent, or (B) there are two subpopulations both initiated with facultative sexuals, that follow different rates of sex.

Figure 2. Outcomes of the simulation runs with competition that occurs between asex and facultative sex (left panels), facultative sex and obligate sex (right panels), and all three types (center panels), for the scenarios A-D as indicated in the rows. Each of the 21 different sex rate values, logarithmically spaced between 0.0001 and 0.5, and 20 different cost of sex values, logarithmically spaced between 0.001 and 0.5, yields one miniature summary plot where the final proportion of asex (black), facultative sex (yellow), and obligate sex (red) phenotypes are indicated from left to right. The full 3-part miniatures are given in the center panels, replaced by 2-part miniatures in the left and right panels where there only two of the potential three subpopulations participate in the competition. Parameter values $s = 0.01$, $\mu = 10^{-5}$.

Figure 3. Outcomes of the simulation runs for the same parameter values and the same stopping criterion as in Figure 2, when two subpopulations initialized with different rates (f_1f_1 and f_2f_2 homozygotes) begin to compete via an exchange of migrants. Each x axis value denotes the rate of sex for f_1, with the next higher value used for f_2; at the rightmost end (where there is no higher value available) f_2 uses 0.75 for its sex rate. Each parameter combination is used three times, and outcomes reported as left-pointing large blue arrows, left-pointing small blue arrows, right-pointing small green arrows, and right-pointing large green arrows, respectively, for 0, 1, 2 and 3 times that the total number of individuals

following the higher rate of sex exceeds the number for the lower rate of sex at the end of the simulation.

Figure 1

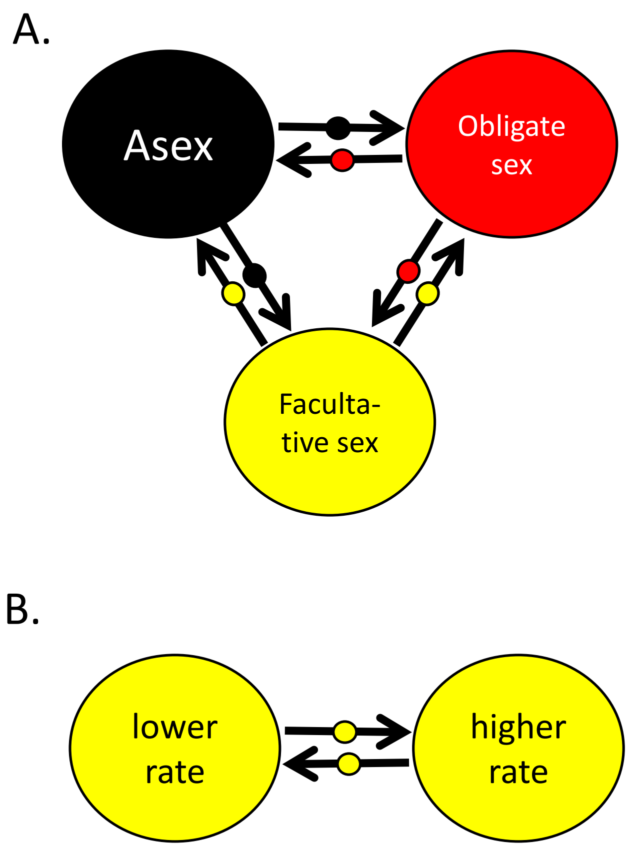
A.
Asex
Obligate sex
Faculta-tive sex
B.
lower rate
higher rate

Figure 2

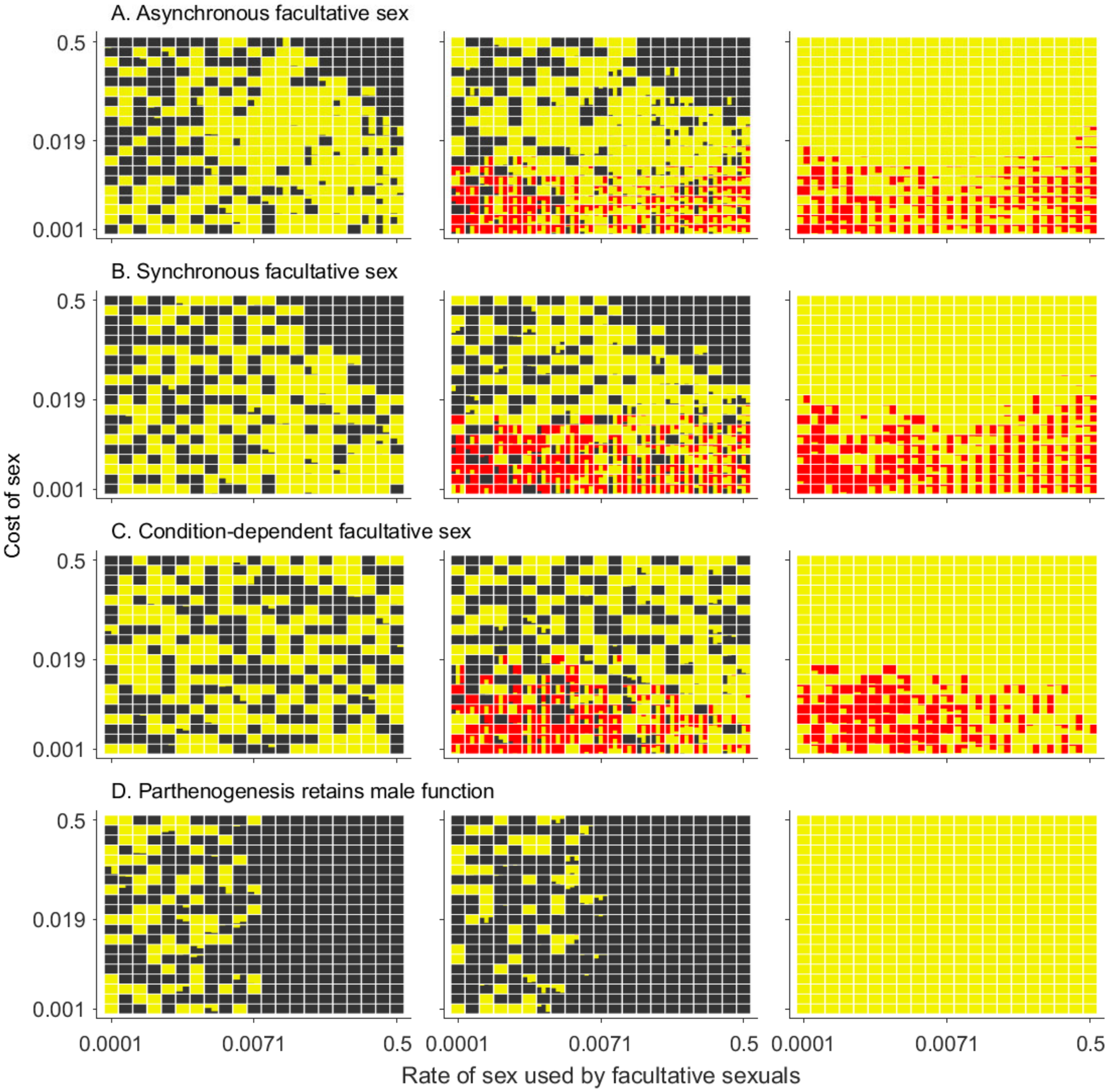

Fig. 2

Figure 3

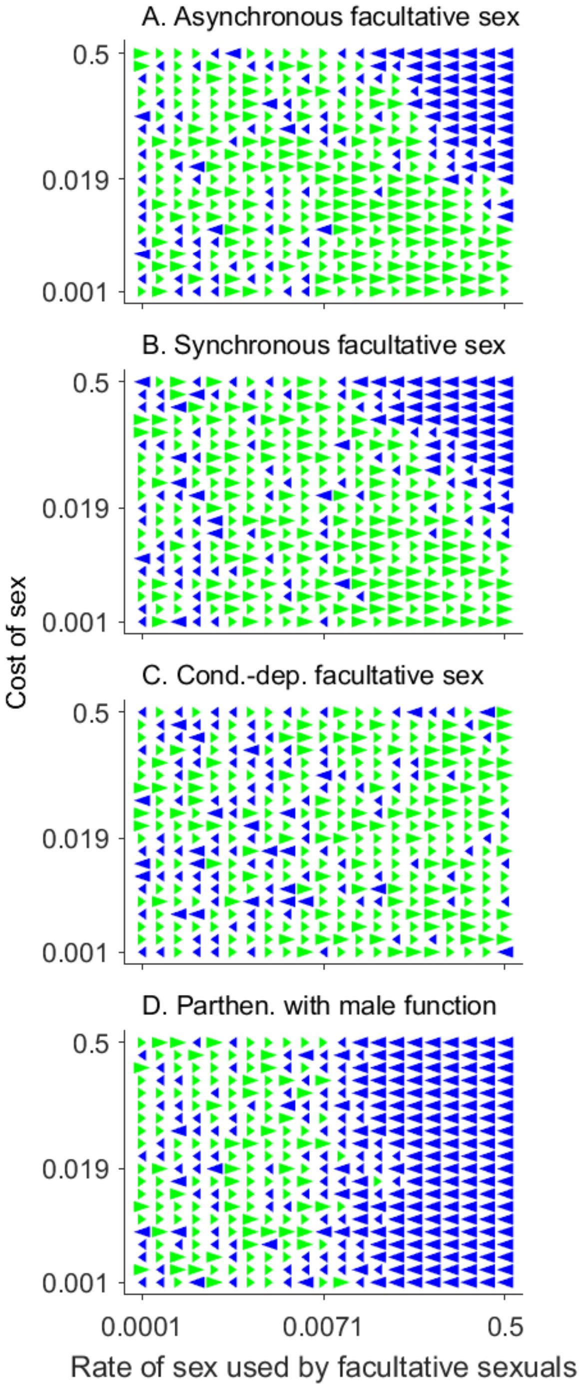

Fig. 3

Supplementary figures