

# Why Sex? and Why only in Pairs?\*

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## Abstract

No single question has been more central to our understanding of sex than the question of why a species reproduces sexually when asexual reproduction avoids the twofold cost of males. Surprisingly, an equally fundamental question has received virtually no attention at all. That is, *why are there no triparental species in which an offspring is composed of the genetic material of three individuals?* Answering this question can have a substantive impact upon our understanding of sex. We show that Kondrashov's (1982) mutational deterministic hypothesis fails to answer this question because it implies that triparental sex always dominates biparental sex, so the former – not the latter – should be observed. By way of contrast, we offer a simplified Red Queen model in which biparental sex is never dominated by triparental sex, quadriparental sex, etc.

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## 1. Introduction

The breadth and variety of methods by which different species reproduce through sex is nothing short of remarkable. Salmon mate once and die; male seahorses carry their young; some species of slime mold have hundreds of mating compatibility classes with intricate rules governing the allowed pairings; female praying mantises eat the male during sex starting with his head, which makes him more enthusiastic. Despite these wildly distinct techniques and the specialized and finely-tuned mechanical adaptations required to carry them out, sexual reproduction displays the following stunning regularity.

Each offspring produced by any known sexual species is produced from the genetic material of precisely *two* individuals. That is, sex is always *biparental*.

The obvious, but overlooked, question is, *Why?* In particular, why are there no triparental species in which an offspring is composed of the genetic material of three individuals? We shall refer to this as the “triparental sex puzzle.”<sup>1,2</sup>

The triparental sex puzzle is more than just an ignored and unexplained empirical regularity. Indeed, a solution to this puzzle is bound to shed light on the purpose of sex itself, a question that remains one of the most important unresolved problems in evolutionary biology. But how is it that, by considering triparental sex, an empirical absurdity, we might obtain a better understanding of sex? The answer is that a complete theory of sex must strike a delicate balance. On the one hand, it must explain why genetic mixing is sufficiently beneficial so that biparental sex overcomes its twofold cost. On the other hand, genetic mixing must not be so beneficial that a further increase in fitness would be obtained from even more of it through triparental sex. Theories that are unable to walk this fine line should be eliminated from consideration.

Our approach is therefore reminiscent of that of R.A. Fisher (1930, p. ix) who eloquently promoted a theoretical approach to biology, an approach that yields greater understanding of reality by considering a wider counterfactual world. To illustrate the necessity of such an approach, Fisher offered the following example.

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<sup>1</sup>Of course, similar questions arise regarding quadriparental sex, etc.

<sup>2</sup>To eliminate any possibility for confusion, we remark that triparental sex *need not* involve triploid individuals with offspring composed of equal contributions from three parents. Triparental sex refers to *any* reproduction system in which each cell of an offspring is composed of genetic material from three parents in some proportions (e.g., a diploid species in which one parent contributes twice as much genetic material as each of the other two).

No practical biologist interested in sexual reproduction would be led to work out the detailed consequences experienced by organisms having three or more sexes, yet what else should he do if he wishes to understand why the sexes are, in fact, always two?<sup>3</sup>

To the best of our knowledge, the possibility of triparental sex has not been given serious consideration. Perhaps this is because one is tempted to dismiss it on the grounds that the associated costs — be they the cost of unproductive males or mating coordination costs — are prohibitive. But, insofar as such arguments have been provided at all, they are unpersuasive. In particular, they fail to take into account the key point that any argument against the transition from biparental sex to triparental sex may be even more persuasive for ruling out the transition from asexual reproduction to biparental sex. Several such arguments are considered in Section 2.

We confront two leading theories for the maintenance of sex with the triparental sex puzzle. The first of these is the mutational deterministic (MD) hypothesis due to Kondrashov (1982, 1988). The second is the “Red Queen” (RQ) hypothesis, models of which have been proposed, for example, by Jaenike (1978), Hamilton (1980), and Hamilton et. al. (1990). Both the MD and RQ hypotheses exploit the fact that sex generates genetic mixing, although they are in sharp disagreement about precisely why genetic mixing is advantageous. Roughly, the MD hypothesis asserts that genetic mixing reduces mutational load, while the RQ hypothesis asserts that it reduces the impact of parasitic attack by increasing genotypic variability. Our main objective is to illustrate that consideration of the triparental sex puzzle may shed new light on both hypotheses.

Beginning with the MD hypothesis, we find that triparental sex has a fitness advantage over biparental sex for all parameter values considered, even accounting for the cost of males. Moreover, this advantage can be substantial when the mutation rate is high enough to permit biparental sex to overcome its twofold cost. Thus, the MD hypothesis **fails to** simultaneously explain **the presence of** biparental sex and the absence of triparental sex.

On the other hand, we present a simplified RQ model that is able to confer an overwhelming advantage to biparental sex over asexual reproduction but that never confers any advantage at all to triparental sex (or to quadriparental sex,

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<sup>3</sup>Perhaps Fisher was glossing over some early evidence of instances of more than two mating compatibility classes. Certainly species with many sexes in this sense have since been discovered. Power (1976) examines the evolutionary rationale for this. Of course, the question of the number of sexes is distinct from the question we are considering here.

etc.) over biparental sex. The model is therefore consistent with the fact that we see biparental, but not triparental, sex.

The interest in this RQ model is *not* in the advantage it is able to confer to biparental sex over asexual reproduction — this, as in typical RQ models, occurs through severe parasitic effects. Rather, it is the RQ model’s ability to confer no additional advantage to triparental sex **that is of interest**. This **key** property is a consequence of the fact that the distribution of genotypes determines the population’s fitness and, as shown in (Perry et. al. (2006)), the equilibrium distribution of genotypes in a population is independent of which sexual system (biparental, triparental, or more) is employed.

The remainder of the paper is organized as follows. Section 2 discusses several potential obstacles to triparental sex: developing genetic machinery, coordination costs, and the cost of males. Section 3 reviews the MD hypothesis, extends Kondrashov’s (1982) model to permit triparental sex, and demonstrates that triparental sex always dominates biparental sex, even accounting for the cost of males. Section 4 provides our simplified RQ model. Section 5 contains a discussion of the possibility that additional costs to triparental sex might be present, and also shows that our Section 3 results concerning the MD hypothesis remain valid from an evolutionary stability point of view. We conclude in Section 6.

## 2. Obstacles to Triparental Sex

There are several obstacles that might prevent a transition from biparental sex to triparental sex. First, the requisite genetic machinery must be developed. Second, there is the cost of coordinating the mating of three individuals rather than two. Finally, just as there is a twofold cost of sex when mating is biparental, one might expect that there must be a “threefold” cost when mating is triparental. We argue that each of these obstacles is minor or absent altogether.

### 2.1. Genetic Machinery

Take first the argument that the absence of triparental sex is due to the difficulty of adapting the cellular mechanisms involved in biparental reproduction to more than two parents.<sup>4</sup> We wish to suggest, on the contrary, that the mechanical

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<sup>4</sup>It has been suggested that triparental reproduction arises in *E. coli* (Fischer-Fantuzzi and Di Girolamo (1961)). These are prokaryotes that exchange DNA via conjugation, which is not considered sex, since there is no meiosis or formation of gametes.

adaptations required for triparental sex are relatively minor. As a starting point, we note that existing cellular machinery is already capable of producing an offspring with more than two parents. Indeed, it seems that offspring with more than two parents must occur with some regularity in nature, for reasons that we now describe.

Consider a well documented case in humans in which two fertilized eggs — usually leading to non identical twins — evidently fused together to produce a single child (N. Yu et. al. (2002)). The otherwise normal child was composed of two types of cells, each derived from one of the fertilized eggs; that is, the child was tetragametic. Now, in this particular case, the two fertilizing sperm cells were each from the same father. However, the same fusion event can presumably occur in a so-called multi-paternal species in which it is not unusual for two eggs to be fertilized by distinct fathers. In this case, the offspring would have *three* parents. Indeed, some of the offspring’s cells would contain genetic material from the mother and one father, while other cells would contain genetic material from the mother and the other father. Thus, it is already feasible in nature for an offspring to have three parents.

The above example, while illustrating the possibility of three parents, is not quite an example of triparental sex because no single cell of the offspring is composed of the genetic material of more than two adults. In particular, the tetragametic individual’s children will have precisely four grandparents, just as in the usual case of biparental sex. On the other hand, a plausible sequence of events *can* lead to fully triparental sex as follows.<sup>5</sup>

Suppose a female mates with two males sequentially, with the first male’s sperm entering her egg first and the second male’s sperm entering the same egg second, creating a triploid zygote.<sup>6,7</sup> The two male ploidies then recombine through the usual process (but without duplication), after which the triploid zygote reduces

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<sup>5</sup>However, none of our arguments hinge upon the precise mechanical process through which triparental sex occurs.

<sup>6</sup>In the sea urchin, for example, an electrical shield reacts quickly to prevent entry into the egg of multiple sperm from a single male. It then fades out and is replaced by a mechanical shield. A similar process of alternating shield activation and deactivation could, in principal, be used to permit entry of just one of each of two males’ sperm, given a time lag between the two matings.

<sup>7</sup>While in many species immediate access to a second male entails no additional cost (see Section 2.2), sperm storage, already found in nature, would render immediate access unnecessary. An extreme example is the female Indian Lizard, who can store sperm for up to six months (see Shanbhag 2003).

to a diploid zygote through absorption, say, of one of the combined ploids from the males. Finally, this diploid zygote containing the female's ploid and the other combined ploid from the males, produces an offspring in the usual way. Each cell of the resulting offspring is therefore composed of the genetic material of one mother and two fathers. Because the fathers' genetic contributions are, on average, equal and are each half that of the mother's, we refer to this reproductive process as  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ -triparental sex, or simply  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex.

Note that each step in the  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex process, except the second, can be carried out by existing genetic machinery. Moreover, the second step appears no less difficult in principle than the recombination and absorption step that routinely takes place in the ordinary process of creating an egg. Thus, an evolutionary pathway to triparental reproduction may entail substantially fewer steps than were required along the path from asexual to biparental reproduction. Consequently, if a fitness advantage, net of any fitness costs, of triparental sex over biparental sex were found to exist, one would expect the same forces of natural selection that led to biparental sex to also bring triparental sex into existence.

## 2.2. Coordination Costs

### 2.2.1. Logistical Coordination Costs

The logistical coordination-cost argument against triparental sex goes back at least to Power's (1976) study of mating-compatibility classes. Power offers some brief remarks aimed at dispensing with the question of why no organism found in nature requires the fusion of three or more gametes to form a zygote, as follows—

...[this is] probably... because of the logistical difficulties of assembling three or more individuals of different sex..., and individuals requiring two or more mating partners for recombination would thus be at a severe disadvantage in terms of energy expenditure and generation time relative to any others which could successfully reproduce with only a single partner.

But is this argument convincing? We think not. After all, the same argument applies with perhaps even greater force against the transition from asexual reproduction to biparental sex, where it must be incorrect. Further, the argument is at odds with the empirical observation that mating behavior often involves the coordination of three or more individuals. Indeed, consider once again multi-paternal

species, where females often give birth, in a single litter, to offspring having different fathers. A brief survey of the literature reveals that this is commonplace, so that, evidently, it is not unusual for several males to all have access to a single female.<sup>8</sup>

A related phenomenon occurs in ants and social bees, whose mating systems require each nest to be founded with the nuptial flight of a virgin queen (Hölldobler and Wilson (1995, p.32)). Each such queen mates at least several times, choosing from a horde of ardent male suitors, and stores the sperm of many distinct males to use for all her future reproduction. Finally, in polyspermic species, such as the comb jelly (*Beroë ovata*), a female’s egg may be penetrated by multiple sperm, one of which is “chosen” to fertilize it (Carre and Sardet (1984)).

In addition to the examples above, one may also consider the many species in which a female typically mates more than once during a single estrus. In all of these cases, the female’s eggs are routinely exposed to the sperm of multiple males. Consequently, for a wide range of species, triparental sex — e.g., where the sperm of two distinct males fertilize a single egg — would entail no additional logistical coordination costs.

### 2.2.2. Fertilization Coordination Costs

Under biparental sex, a particular egg made available for fertilization presumably has a lower probability of actually being fertilized – since sperm and egg may fail to “coordinate” a meeting – than under asexual reproduction. There must therefore be a small cost of eggs (and of sperm) wasted like this through biparental sex. Such wastage seems bound to be increased by triparental sex. On the other hand, there are many eggs and even more sperm, and this waste need not greatly affect the overall probability of some zygote being formed, with either biparental or triparental sex. Indeed, most of the cost of bearing an offspring usually takes the form of energetic transfers to the embryo after fertilization, in the womb or after birth. Accordingly, and consistent with the assumption implicit in Kondrashov

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<sup>8</sup>For example, the fraction of litters displaying multi-paternity is 75% for feathertail gliders – *Acrobates pygmaeus* (Paaott et. al. (2005)); 69% for Bicknell’s thrush – *Catharus bicknelli* (Goetz et. al. (2003)); 62.5% for land snails – *Helix aspersa* (Evanno et. al. (2005)); 35% for garter snakes – *Thamnophis sirtalis* (Garner et. al. (2002)); 20% for spur-thighed tortoise – *Testudo graeca* (Roques et. al. (2004)); and 20% for thalassinidean ghost shrimp – *Callichirus islagrande* (Lanie et. al. (2004)).

(1982) in particular, we set this cost to zero.<sup>9</sup>

### 2.3. The Cost of Males

Maynard Smith (1978) identified the “twofold cost of sex,” namely, that a sexual population with a one to one ratio of unproductive males to females produces half as many offspring as an equally-sized asexual population. One might then naturally expect triparental sex — involving two unproductive males and one female — to display a threefold cost of males relative to asexual reproduction. But, remarkably, triparental sex can be achieved at only a *twofold* cost. Put differently, triparental sex can be achieved at *no additional cost of males* relative to biparental sex. We now explain why.

Consider a population of males and females in which reproduction takes place according to the  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex process described in Section 2.1. Because the cost of males is determined not by the ratio of males to females in each mating instance but, rather, by the *population* ratio of males to females, determining the population ratio is central. We therefore turn to Fisher’s (1930, pp.142-43) celebrated equilibrium argument. Applying the same logic here, we note first that the total reproductive value of all of the males in any generation is precisely equal to that of all the females in that generation. This is because, under  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex, all of the females supply half of the genes of all future generations. But then the remaining half must be supplied by all of the males. Consequently, as Fisher argued, equilibrium requires the offspring sex ratio to equate parental expenditure on male and female offspring. Maintaining the usual assumption that offspring of either sex are equally costly to raise to maturity, we conclude that the equilibrium sex ratio must be one.<sup>10</sup> But this means that the cost of males is twofold, precisely as in the case of biparental sex. That is,  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex entails no additional cost of males relative to biparental sex.

The above discussion of the potential obstacles to triparental sex can be summarized as follows.

1. Adapting the genetic machinery for biparental sex to triparental sex seems a minor obstacle relative to the development of that machinery in the first place.

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<sup>9</sup>In fact, any fertilization cost of  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex can be driven to zero by maintaining biparental sex as a default option in case the egg is fertilized by only one sperm. A related default option occurs in *C. elegans*, who reproduce asexually if they do not find a suitable male.

<sup>10</sup>Therefore, each male mates with two females and vice versa.



2. There is no additional coordination cost to triparental sex over biparental sex in the many species already coordinating three or more individuals for mating.
3. Triparental sex can be achieved without any additional cost of males relative to biparental sex.

### 3. The Mutational Deterministic Hypothesis

A leading explanation for the maintenance of sex in large populations is Kondrashov's (1982, 1988) mutational deterministic hypothesis in which sex is advantageous because it halts the otherwise steady accumulation of harmful mutations.<sup>11</sup> In this section, we present a challenge to this theory based upon the difficulty it seems to have in resolving the triparental sex puzzle. We begin with a brief review.

Kondrashov (1982) makes the following simplifying assumptions. An individual's genome has infinitely many loci between which there is no linkage. Mutations at all loci are equally harmful so that an individual offspring's survival probability is determined by its total number of mutations. Specifically, an offspring with  $i < K$  mutations survives with probability  $s_i = 1 - (\frac{i}{K})^\alpha$ . Offspring with  $K$  or more mutations are not viable. Finally, as individuals develop into adults, they independently receive additional mutations according to a Poisson distribution with mutation rate  $\mu$ , where the probability that any particular locus receives a mutation is zero.<sup>12</sup>

In an asexual population, an offspring inherits its parent's mutations and is then subject to selection. If it survives, it receives mutations from the Poisson process, has offspring of its own, and dies. The process then repeats with the next generation. As shown in Kondrashov (1982), the equilibrium fitness (i.e., the equilibrium fraction of surviving offspring) in an asexual population is  $e^{-\mu}$ , regardless of the values of  $K$  and  $\alpha$ .<sup>13</sup>

In a sexual population, the life-cycle is mutations-recombination-selection-mutations. As in the asexual case, individuals live for a single generation. Let  $q_i$  denote the frequency of individuals in a given generation with  $i$  mutations after

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<sup>11</sup>The first theory of this kind relied upon a finite population and is due to Müller (1964).

<sup>12</sup>These additional mutations do not affect survival, but may of course be passed on to one's offspring, affecting its survival.

<sup>13</sup>See also Kimura and Maruyama (1966).

selection. After mutations arrive according to the assumed Poisson process, the fraction of individuals with  $i$  mutations is

$$q'_i = e^{-\mu} \sum_{j=0}^i q_j \frac{\mu^{i-j}}{(i-j)!}. \quad (3.1)$$

Now, because no two matched individuals have more than one mutation in total at each locus, the frequency with which an offspring from parents having  $n$  and  $m$  mutations has  $i$  mutations is  $\binom{n+m}{i} (\frac{1}{2})^{n+m-i} (\frac{1}{2})^i$ . Consequently, the fraction of offspring having  $i$  mutations after recombination is,

$$q''_i = \left(\frac{1}{2}\right)^{n+m} \sum_{n+m \geq i} q'_n q'_m \binom{n+m}{i}.$$

Finally, since offspring with  $i < K$  mutations survive with probability  $s_i$  and only offspring with fewer than  $K$  mutations survive, the fraction of individuals with  $i < K$  mutations after selection is,

$$q'''_i = \frac{s_i q''_i}{s_0 q''_0 + \dots + s_{K-1} q''_{K-1}}, \quad (3.2)$$

where  $s_0 q''_0 + \dots + s_{K-1} q''_{K-1}$  is the fitness of the population, or equivalently, the fraction of surviving offspring. The equilibrium distribution of mutations is characterized by the additional condition that  $q_i = q'''_i$  for  $i = 0, 1, \dots, K-1$ , from which one can also obtain the population's equilibrium fitness.

Kondrashov demonstrates that the equilibrium fitness of a sexual population exceeds twice that of an asexual population (and hence accounts for Maynard Smith's twofold cost) so long as the mutation rate is sufficiently high. The magnitude of the genomic mutation rate is now the focus of an ongoing debate.

### 3.1. Triparental Sex

Let us now adapt Kondrashov's model to allow for the possibility of  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  sex as described in the previous section, where the life cycle is again mutations-recombination-selection-mutations. Once again, let  $q_i$  denote the fraction of individuals with  $i$  mutations after selection, so that after mutations arrive the fraction of individuals with  $i$  mutations is  $q'_i$  given by equation (3.1) just as before. The difference comes at the recombination stage.

Consider a parental match in which the mother has  $m$  mutations and the two fathers have  $n$  total mutations. The offspring can have  $i$  mutations if for some  $m' \leq m$  and some  $n' \leq n$ , it receives  $m'$  from the mother and  $n'$  from the fathers, where  $m' + n' = i$ . Therefore, because the three parents have no more than one mutation in total at each locus, the frequency with which an offspring has  $i$  mutations in this case is,

$$r_{m,n}^i = \sum \binom{m}{m'} \binom{n}{n'} \left(\frac{1}{2}\right)^m \left(\frac{1}{4}\right)^{n'} \left(\frac{3}{4}\right)^{n-n'},$$

where the sum is over  $m' \leq m$  and  $n' \leq n$  such that  $m' + n' = i$ . Consequently, the fraction of offspring having  $i$  mutations after recombination is,

$$q_i'' = \sum_{n+m \geq i} q_m' \left( \sum_{j=0}^n q_j' q_{n-j}' \right) r_{m,n}^i.$$

Finally, the fraction of individuals having  $i < K$  mutations after selection is  $q_i'''$ , which as before, is related to  $q_i''$  through equation (3.2).

The equilibrium distribution of mutations is again characterized by the additional condition that  $q_i = q_i'''$  for  $i = 0, 1, \dots, K-1$ , from which one can also obtain the population's equilibrium fitness.

### 3.2. The Benefits to Triparental Sex

We now compare the equilibrium fitness of a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population with that of a biparental population using the deleterious mutation model above. Our main finding is that  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex dominates biparental sex for all parameter values considered. Clearly, this finding poses a challenge to the deleterious mutation theory of sex.

As in Kondrashov (1982), three choices of the fitness function parameter,  $\alpha$ , are considered. At one extreme, when  $\alpha = \infty$ , we obtain the threshold fitness function in which an individual's probability of survival is 1 so long as the individual has fewer than  $K$  mutations. As always, an individual with  $K$  or more mutations is not viable. At the other extreme, when  $\alpha = 1$ , we obtain the linear fitness function,  $s_i = 1 - \frac{i}{K}$ , in which an individual's probability of survival diminishes at a constant rate per additional mutation until, at  $K$  mutations, the probability of survival becomes zero. Between these two extremes is the case in which each additional mutation reduces one's probability of survival by more than

the reduction caused by the previous mutation. Like Kondrashov, we explore this intermediate possibility by considering  $\alpha = 2$ , which yields the quadratic fitness function,  $s_i = 1 - (\frac{i}{K})^2$ . The values of  $K$  considered here are taken from the literature. For example, Kondrashov (1982) considers  $K = 5, 20$ , and  $80$ , while Howard (1994) considers  $K = 60$ .

$\mu$	$K = 5$	$K = 20$	$K = 60$	$K = 80$	$\alpha$
1	2.1	1.0	0.4	0.3	$\infty$
	2.3*	1.6*	0.7*	0.5*	2
	2.0*	1.4*	0.6*	0.5*	1
1.5	3.4	1.9	0.8	0.7	$\infty$
	3.5*	2.8	1.4	1.1	2
	3.2*	2.7*	1.3*	1.0*	1
2	4.8	3.0	1.4	1.1	$\infty$
	4.8	4.2	2.3	1.8	2
	4.4*	4.1	2.2	1.7	1
3	7.4	5.6	2.8	2.2	$\infty$
	7.1	7.0	4.3	3.6	2
	6.7	7.1	4.3	3.6	1
4	9.8	8.6	4.5	3.6	$\infty$
	9.3	10.1	6.6	5.6	2
	8.8	10.2	6.7	5.7	1
6	14.2	15.3	8.9	7.3	$\infty$
	13.2	16.7	11.8	10.2	2
	12.6	16.8	12.0	10.4	1
8	17.8	22.7	14.4	11.9	$\infty$
	16.5	23.7	17.7	15.5	2
	15.9	23.7	18.0	15.7	1

Table 1: % Advantage of Triparental Sex

Table 1 shows the advantage of  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  sex over biparental sex. Each entry in the table is the **percentage amount by which** the equilibrium fitness of a  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  sexual population **exceeds that of a** biparental population for a particular vector of parameters,  $(\mu, K, \alpha)$ . Because the only cost to sex in Kondrashov's model is the cost of males, there is no cost to  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  sex over biparental sex.<sup>14</sup> Consequently,

<sup>14</sup>This was shown in Section 2.3.

**each entry is also the percentage amount by which the growth rate of the triparental population exceeds that of the biparental population.** An asterisk indicates that biparental sex fails to overcome its twofold cost relative to asexual reproduction in that cell.

**Every entry in Table 1 is positive, indicating that** a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population always grows faster than a biparental population. Moreover, when biparental sex overcomes its twofold cost — indicated by cells without asterisks — the advantage to triparental sex can be substantial. For example, with intermediate selection and a mutation rate of 2, a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  population grows between 1.8% and 4.8% faster than a biparental population, implying a relative doubling time of between 14 and 39 generations. The MD hypothesis therefore does not appear to provide an explanation for the presence of biparental sex and the absence of triparental sex. Section 5 provides further discussion.

#### 4. A Red Queen Model

A second major class of theories for the maintenance of sex is the class of Red Queen (RQ) theories. These explain sex as a way for a host organism to maintain parity in the race against parasites. Parasites evolve rapidly to disproportionately infect any genotype that becomes common. An asexual population, in which all individuals have the same genotype, might well then eventually be annihilated by the parasite. In contrast, a sexual population is composed of a variety of genotypes, which sex keeps remixing. Sex is helpful because it not only regenerates genotypes that were once wiped out by the parasite, it also prevents any particular genotype from dominating the population, thereby reducing the potential reduction in the population from any single parasitic attack. (See, for example, Jaenike (1978), Hamilton (1980), and Hamilton, Axelrod, and Tanese (1990).)

We next present a highly stylized RQ model in which biparental sex dominates asexual reproduction when parasites cause a sufficient reduction in host fitness — a mechanism that is well understood. The interest in the model lies in the fact that, regardless of the fitness effects of parasites on their hosts, triparental sex does not dominate biparental sex. Consequently, this RQ model — and, possibly, richer RQ models as well — can simultaneously explain the presence of biparental sex and the absence of triparental sex.

Consider an infinite population of hosts and an infinite population of parasites. The host population is composed of a distribution of genotypes. For each possible genotype in the host population there is a matching genotype in the parasite

population. Occasionally, the two populations interact, when a randomly chosen individual in the host population is infected with the full genotypic range of parasites. Since this includes the particular genotype matching that of the individual, this causes an epidemic in the host population killing a fraction  $\delta$  (for “death”) of all individuals in the host population with that genotype.<sup>15</sup> There is no selection in the host population apart from that arising in these occasional interactions with the parasites; it is unimportant whether there is any selection in the parasite population, as long as the full range of genotypes is maintained.

Consider the most extreme case in which the parasite is most virulent, i.e., where  $\delta = 1$ , so that *all* individuals with a particular genotype are killed in each epidemic. First, note that an asexual population will become extinct upon its first interaction with the parasites, or after finitely many interactions if the initial distribution of genotypes is nondegenerate. What will be the fate of a biparental species? Assuming that the time between epidemics is not too short, the host distribution of genotypes will be approximately in Robbins proportions just prior to contact with the parasites. Immediately after contact with the parasites, all individuals of one particular genotype will be eliminated. But because the population was originally in Robbins proportions, all alleles remain present. On the other hand, the distribution of alleles is no longer the same and so the population will converge to its new Robbins proportions prior to its next contact with the parasites, and so on.

The overall dynamics of a biparental population can therefore be summarized as follows. Beginning from Robbins proportions, all individuals of some randomly chosen genotype are killed by an epidemic. The population converges to its new Robbins proportions. The next epidemic occurs, once again killing all individuals from a randomly chosen genotype, and so on indefinitely. Thus, a biparental population survives forever, and the effect on population fitness of each epidemic is determined by these successive Robbins proportions.

The key observation is that the above dynamics are unaffected by whether sexual reproduction is biparental or  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ . This is because, for any given distribution of alleles, the distribution of genotypes in a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population converges to the Robbins proportions just as it does in a biparental population (Perry et. al. (2006)). Hence, because our RQ dynamics depend only on the derived sequence of Robbins proportions, the population growth rate will be the same with either sexual system.

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<sup>15</sup>The most likely epidemic event is that in which the most common genotype in the population is infected.

What if  $\delta < 1$ ? Once again the RQ dynamics will depend only upon the derived sequence of Robbins proportions, which remain independent of which sexual system is employed. Consequently, triparental sex and biparental sex yield the same population growth rates. The only difference concerns the relative growth rate of the biparental and asexual populations, and, as might be expected, a biparental population can overcome its twofold cost only if  $\delta$  is sufficiently close to 1.<sup>16</sup> So, for the simplified RQ model described here, biparental sex can dominate asexual reproduction, but  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex can never dominate biparental sex.

In a richer model, the interactions between the host and parasite may be more frequent, and the host population need not arrive approximately at its Robbins proportions between successive epidemics. The analysis is then more complex. However, numerical simulation suggests that the key result is robust. That is, there remains no significant difference between the fitness of a biparental population and that of a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population; indeed, the small differences in fitness that do arise do not systematically favor either system over the other.

What about the maintenance of biparental sex against mating systems other than  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex, such as quadriparental sex, etc.? The results described here remain valid. In fact, convergence to Robbins proportions is an extremely robust result that can be shown to hold for a large class of generalized mating systems (Perry et. al. (2006)). The present results therefore continue to hold for all such mating systems. RQ theories, despite their flaws, are nonetheless capable of simultaneously explaining the maintenance of biparental sex against asexual reproduction and also against  $N$ -wise sex for all  $N \geq 3$ .

## 5. Discussion

### 5.1. The MD Hypothesis, Additional Costs of Sex, and High Mutation Rates

Returning to the MD hypothesis, recall that the analysis in Section 3 maintains the standard assumption in the related literature that the only cost of sex is the cost of unproductive males, with the implication that there is no cost to  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex relative to biparental sex (Section 2.3), from which the uniform advantage of

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<sup>16</sup>RQ models have, of course, been criticized for requiring severe effects from parasites (May and Anderson (1983, Section 4), and we do not address this difficulty here. Rather, our interest lies merely in highlighting the intriguing ability of RQ models to explain why triparental sex has no advantage over biparental sex.

$\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex over biparental sex follows (Table 1).

Let us now place triparental sex at an unfair disadvantage by supposing that there are small additional costs to triparental sex, but no additional costs to biparental sex. It is then no longer the case that  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex uniformly dominates biparental sex. Nonetheless, the analysis of Section 3.2 remains useful. Indeed, it still suggests that, contrary to current thinking, not only do low mutation rates – e.g., below 1-2 (Charlesworth (1990), Howard (1994), Kondrashov (1988)) – constitute evidence against the MD hypothesis, but *high* mutation rates too, may constitute evidence against it.

That is, in Table 1, the higher is the mutation rate, the larger is the advantage to  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ -triparental sex over biparental sex. With intermediate selection, for example, a mutation rate of 3 is already high enough to imply that a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population grows 3.6% to 7.1% faster than a biparental population, implying a relative doubling time of between 10 and 20 generations. Given such large advantages to triparental sex, explaining its absence under the MD hypothesis would require the additional cost of triparental sex to be substantial. If, especially for the wide range of species described in Section 2.2, only small costs to triparental sex can be identified, then mutation rates above 3 or 4 might constitute evidence against the MD hypothesis in the same way that mutation rates below 1 or 2 are now recognized to. This may be especially relevant in light of current mutation rate estimates of between 3 and 6 in chimpanzees (Keightley and Eyre-Walker (2000))<sup>17</sup>, some of whom (e.g. bonobos) are highly promiscuous so that coordination costs – for triparental over biparental sex – are not an issue.

## 5.2. Evolutionary Stability and the MD Hypothesis

So as to permit the most direct comparison with Kondrashov (1982), we have couched all of our Section 3.2 relative fitness calculations in terms of population equilibrium values. However, it is natural to wonder whether a small fraction of triparental females introduced into an equilibrated biparental population will eventually take over. The answer is in the affirmative.

We begin by seeding an equilibrated biparental population with a small fraction of females possessing one copy of a dominant triparental gene for  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual reproduction.<sup>18</sup> Their distribution of mutations coincides with that of the biparental

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<sup>17</sup>The mutation rate of 6 is obtained by multiplying by 2 the estimate in Keightley and Eyre-Walker's Table 1. As they point out, this is to account for mutations in noncoding DNA.

<sup>18</sup>It is assumed that the female has all of the adaptations required for triparental sex and that



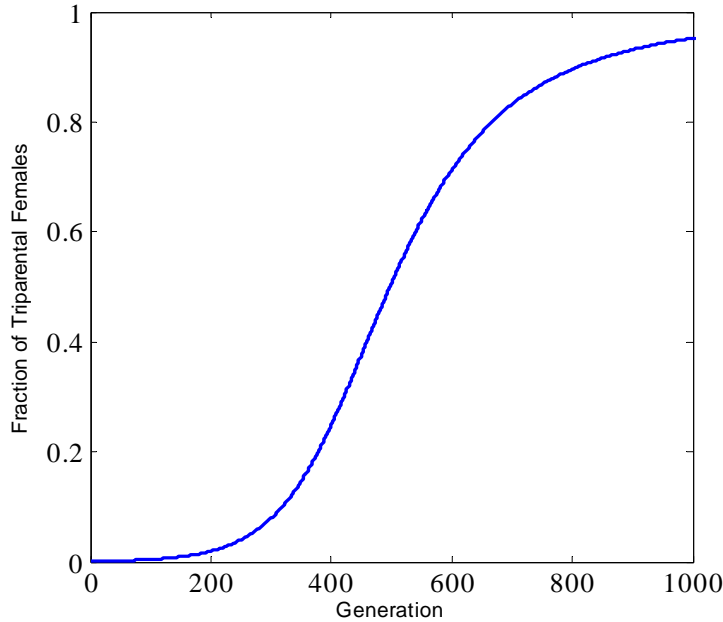


Figure 5.1:  $f = 0.001$ ,  $\mu = 3$ ,  $K = 20$ ,  $\alpha = 2$

population. Males can mate with both biparental and triparental females. The triparental gene is expressed only in females, although males can pass the gene on to both male and female offspring, the latter of whom reproduce triparentally through  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex.

In all runs, the fraction of triparental females – i.e., those with at least one copy of the triparental gene – increase with each generation, as does the fitness of the population. The increase in fitness benefits not only  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual females, but biparental females as well, because each mates with a fitter population of males. But biparental offspring nonetheless remain at a relative fitness disadvantage and *the biparental population is always inevitably driven to extinction*.<sup>19</sup>

At low mutation rates, driving the biparental population to extinction can take many generations. However, many fewer generations may be needed for the

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males cannot prevent triparental sex.

<sup>19</sup>In contrast, when a triparental sexual population is in equilibrium, biparental sex cannot invade.

triparental population to become “visible” – say, at 1% or even at 0.1% of the population – and, because such visibility is contrary to empirical observation, this would suffice to cast doubt on the MD hypothesis. A particular example of one of our runs is shown in Figure 5.1, where  $f$  denotes the initial number of females, as a fraction of the population, possessing a single copy of the triparental gene.

## 6. Conclusion

In this paper, we have demonstrated that there are rich returns to addressing the counterfactual question: Why are there always **just** two parents? We **addressed** this question by **adapting** theoretical approaches that have previously been used to answer the more obvious question: Why is there sex at all?

Within Kondrashov’s deleterious mutation theory – where it is well-known that high genomic mutation rates are needed for biparental sex to overcome its twofold cost over parthenogenesis – what we found deepened the mystery. Triparental sex always dominates biparental sex and high genomic mutation rates only serve to increase this advantage. With all three options available, either parthenogenesis would be best or triparental sex would be best. Accordingly, biparental sex should not be observed.

In contrast, there is a ray of hope with the Red Queen host-parasite model. In this case, biparental sex can have even an overwhelming advantage over parthenogenesis, yet there is no further gain from more than two parents.

This paper will have succeeded if it induces theoretical biologists who ask “why sex?” to also ask “...and why only in pairs?” A complete theory must answer both of these questions simultaneously.

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