

# Why sex? and Why only in pairs?

Motty Perry<sup>1,\*</sup>, Philip J. Reny<sup>2,\*</sup> & Arthur J. Robson<sup>3,\*</sup>

Understanding the purpose of sex remains one of the most important unresolved problems in evolutionary biology. Two leading theories of sex are the mutational deterministic hypothesis that sex reduces mutational load, and the Red Queen hypothesis that sex reduces the impact of parasitic attack by increasing genotypic variability. To distinguish between these theories, we ask: *Why are there no triparental species in which an offspring is composed of the genetic material of three individuals?* A correct theory must confer an advantage to biparental sex without conferring an additional advantage to triparental sex. We show that the mutational deterministic hypothesis fails in this regard because it implies that a particular triparental system dominates biparental sex, so the latter should never be observed. In contrast, we show that the Red Queen hypothesis is able to explain biparental sex without conferring an advantage to triparental sex.

“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?”

R. A. Fisher, *The Genetical Theory of Natural Selection*, Clarendon Press, 1930.

The breadth and variety of methods by which different species reproduce through sex is nothing short of remarkable. Nonetheless, sexual reproduction displays a stunning regularity.

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<sup>1</sup>Department of Economics and Center for the Study of Rationality, The Hebrew University of Jerusalem, Jerusalem, 91904 Israel and Department of Economics, The University of Chicago, Chicago, IL 60637.<sup>2</sup>Department of Economics, The University of Chicago, Chicago, IL 60637.<sup>3</sup>Department of Economics, Simon Fraser University, Burnaby, BC, Canada V5A-1S6.

\*These authors contributed equally to this work.

Each sexually produced offspring of any known 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?

Answering this question – and similar questions regarding quadriparental sex, etc. – is bound to shed light on the purpose of sex itself, one of the most important unresolved problems in evolutionary biology (*1, 2*). Indeed, a complete theory of sex must strike a delicate balance. On the one hand – as is well known – it must explain why genetic mixing is sufficiently beneficial so that biparental sex overcomes the twofold cost of males it suffers because an equally-sized asexual population would grow twice as fast (*3*). On the other hand – and this point is central here – genetic mixing must not be so beneficial that a further increase in fitness would be obtained from even more of it through triparental sex.

Little or no attention has been paid to the possibility that a theory of biparental sex might inadvertently confer an advantage to triparental sex. Perhaps this is because one is tempted to dismiss triparental sex 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 below.

The present paper considers whether either of the two leading theories for the maintenance of biparental sex is consistent with the absence of triparental sex. The first of these theories is the mutational deterministic (MD) hypothesis (4, 5). The second is the “Red Queen” (RQ) hypothesis, of which several models have been proposed (6-8). 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.

Under the MD hypothesis, we find that a particular triparental system involves no additional cost of males, yet has a fitness advantage over biparental sex for all parameter values considered. Moreover, this advantage can be substantial when the mutation rate is high enough to permit biparental sex to overcome its twofold cost. The MD hypothesis therefore 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 confers an overwhelming advantage to biparental sex over asexual reproduction but confers no advantage at all to triparental sex (or to quadriparental sex, etc.) over biparental sex. The RQ hypothesis therefore is not at odds with the presence of biparental sex and the absence of triparental sex.

### **Triparental sex**

Triparental sex is said to occur when each cell of an offspring is composed of the genetic material of three parents. We will focus upon a particularly significant triparental system where an offspring in a diploid population receives half of its genetic material from its mother and one-quarter from each of its two fathers. This system is significant because it involves no additional cost of males over biparental sex, as is explained below, a property that is not true of a system where each of three parents contribute equally. While none of our arguments hinge upon the precise mechanical process through which this occurs, it might be helpful to consider the following sequence of events. The 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, as can occur in polyspermic species such as the comb jelly, *Beroë ovata* (9). The two male ploid sets then recombine through the usual process (but duplication is unnecessary), after which one of the two combined ploid sets is dispensed with. The result is a diploid zygote containing the female's ploid and a combined ploid from the males. This diploid zygote then produces an offspring in the usual way. Each cell of the 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. Before proceeding further, let us address several possible arguments against this triparental system.

First, there is the obstacle of developing the requisite genetic machinery. But

note that each step in the above  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  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 step that routinely takes place in the ordinary process of meiosis. 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.

Second, one might argue that the costs of coordinating the mating of three individuals over just two are prohibitive (10). However, 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 three or more individuals. For example, in multi-paternal species, of which there are many, females often give birth, in a single litter, to offspring having different fathers (11-16). 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 (9). Finally, consider any of 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 coordination costs.

Thirdly, there is 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 (3). One might then naturally expect  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex — involving two unproductive males and one female — to display a threefold cost of males relative to asexual reproduction. But, remarkably,  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex results in only a *twofold* cost. Put differently,  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  triparental sex involves *no additional cost of males* relative to biparental sex. We now explain why.

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 celebrated equilibrium argument (17). Applying the same logic to  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex, we note first that the total reproductive value of all of the males in any generation is precisely equal to that of all of 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 — each male therefore mates with two females and vice versa. 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 no-additional-cost-of-males property does not hold in a triparental triploid population in which the mother and two fathers each contribute a single ploid to the offspring. In such a system, because all females supply only one-third

of the genes of all future generations, Fisher’s argument implies that parental expenditure on males must be twice that on females. Equal offspring costs then imply twice as many males as females, and hence a threefold cost of males. Under all MD hypothesis parameter values considered here, this additional 1.5-fold cost outweighs the benefits of the additional mixing, so that  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex has a higher overall fitness.

Since  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex is not observed in nature, it must not have a fitness advantage over biparental sex. We now show that the MD hypothesis is not consistent with this requirement.

### **The mutational deterministic hypothesis**

A leading explanation for the maintenance of sex in large populations is Kondrashov’s mutational deterministic hypothesis in which sex is advantageous because it halts the otherwise steady accumulation of harmful mutations (4, 5). The first theory of this kind was due to Müller, but relied upon a finite population (18, 19).

Kondrashov assumes the following (4). An individual’s genome has infinitely many loci between which there is no linkage. Mutations at all loci are equally harmful. 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. These additional mutations do not

affect survival, but may be passed on to one's offspring, affecting its survival.

Kondrashov's analysis of a biparental sexual population is as follows. The life-cycle is mutations-recombination-selection-mutations. Individuals live for a single generation. Let  $q_i$  denote the fraction of individuals in a given generation with  $i$  mutations after selection. After mutations arrive according to the Poisson process, the fraction of individuals with  $i$  mutations is

$$q'_i = e^{-\mu} \sum_{j=0}^i q_j \frac{\mu^{i-j}}{(i-j)!}. \quad (1)$$

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  $\binom{n+m}{i} \left(\frac{1}{2}\right)^{n+m-i} \left(\frac{1}{2}\right)^i$ . Consequently, the fraction of offspring having  $i$  mutations after recombination is,

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

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,

$$q'''_i = \frac{s_i q''_i}{s_0 q''_0 + \dots + s_{K-1} q''_{K-1}}, \quad (2)$$

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.

We now adapt Kondrashov's biparental analysis to a triparental  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual population. As in the biparental case, the life cycle is mutations-recombination-selection-mutations, and we again let  $q_i$  denote the fraction of individuals with  $i$  mutations after selection. As before, after mutations arrive, the fraction of individuals with  $i$  mutations is  $q_i'$  given by equation (1).

Consider a triparental 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 their offspring have  $i$  mutations 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 (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.

Let us now compare the equilibrium fitness of a  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  sexual population with that of a biparental population. The values of  $\alpha = 1, 2, \infty$  and  $K = 5, 20, 60, 80$  considered here are taken from the literature (4, 20).

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. Consequently, 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 (i.e.,  $\alpha = 2$ ) 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 provide an

explanation for both the presence of biparental sex and the absence of triparental sex.

$\mu$	$K = 5$	$K = 20$	$K = 60$	$K = 80$	$\alpha$
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
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

Also, the higher is the mutation rate, the larger is the advantage to  $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$  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. Thus, contrary to current thinking, not only do low mutation rates – e.g., below 1-2 (5, 20, 21)– constitute evidence against the MD hypothesis, but *high* mutation rates too constitute evidence against it. And indeed, genomic mutation rate estimates of between 3 and 6 have been found, for example, in

chimpanzees (22).

To permit a direct comparison with the literature, Table 1 provides relative *equilibrium* fitnesses of triparental and biparental populations. However, to further illustrate the inability of the MD hypothesis to explain the absence of triparental sex, we also establish that a small fraction of triparental females introduced into an equilibrated biparental population will eventually take over.

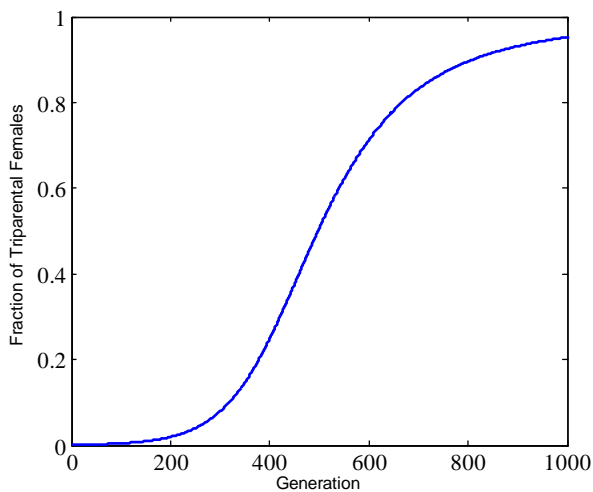


Figure 1:  $f = 0.001$ ,  $\mu = 3$ ,  $K = 20$ ,  $\alpha = 2$

An equilibrated biparental population is seeded with a small fraction of females each possessing one copy of a dominant triparental gene for  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual reproduction. Their distribution of mutations is that of the biparental population. Males can mate with biparental and triparental females. The triparental gene is expressed only in females, although males can pass it on to male and female offspring, the latter then reproducing 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 – increases with each generation, and *the biparental population is driven to extinction*. A particular example of one of our runs is shown in Figure 1, where  $f$  denotes the initial number of females, as a fraction of the population, possessing a single copy of the triparental gene. In contrast, when a triparental sexual population is in equilibrium, biparental sex cannot invade.

### **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 (6-8). Below we present a simplified RQ model in which biparental sex dominates asexual reproduction because parasites occasionally cause a severe reduction in the fitness of a random genotype in the host population – a mechanism that is well understood. The interest in the model lies in the fact that, despite the severe fitness effects of parasites, triparental sex does not confer any additional advantage over 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 para-

sites. Since this includes the particular genotype matching that of the individual, this causes an epidemic in the host population killing all individuals with that genotype.

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? If the time between epidemics is not too short, the host distribution of genotypes will be approximately in Robbins proportions – i.e., the product of the marginal distributions of alleles, locus by locus – just prior to contact with the parasites (23). Immediately after contact, all individuals of one genotype will be eliminated. But because the population was in Robbins proportions, all alleles remain present. However, the distribution of alleles is no longer the same and so the population will converge to its new Robbins proportions before its next contact with the parasites.

The overall biparental dynamics is therefore as follows. Beginning from Robbins proportions, all individuals of a random genotype are killed by an epidemic. The population converges to its new Robbins proportions. The next epidemic occurs, killing all individuals of a random genotype, and so on. Thus, a biparental population survives forever, and population fitness against epidemics is determined by the successive Robbins proportions.

The key observation is that the dynamics are unaffected by whether sexual reproduction is biparental or  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual. This is because, for any distribution of alleles, it can be shown that the distribution of genotypes in a  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sexual

population also converges to the Robbins proportions just as in a biparental population. Hence, because the RQ dynamics depend only on the derived sequence of Robbins proportions, the population growth rate will be the same with either sexual system. So, biparental sex can dominate asexual reproduction, but  $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$  sex can never dominate biparental sex. Consequently, in contrast to the MD model, biparental sex dominates triparental sex here if the latter involves even an arbitrarily small extra cost.

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, but numerical simulation suggests that the key result is robust. What about 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. Indeed, convergence to Robbins proportions is an extremely robust result that holds for a large class of generalized mating systems and the present results therefore continue to hold.

## **Discussion**

There are rich returns to addressing the question: “Why is sex never triparental?”

Under the MD hypothesis, 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 RQ hypothesis. Using a deliberately

simplified Red Queen model, we have shown that biparental sex can have even an overwhelming advantage over parthenogenesis, yet there is no further gain from more than two parents.

These results demonstrate that those who ask “why sex?” should also ask “...and why only in pairs?” Answering the second question can distinguish between otherwise equally plausible answers to the first.

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