

Testing theories of sex against the observation that sex is biparental

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Abstract

Understanding the purpose of sex remains one of the most important unresolved problems in evolutionary biology. One of the reasons for its unresolved status is that many competing theories have proven difficult to reject. In the spirit of Fisher (1930), we propose that a theory of sex must be capable of predicting that sexually produced offspring have only two parents, not three or more. As an example of the power of this approach, it is shown that the mutational deterministic (MD) hypothesis fails this test. That is, the MD hypothesis implicitly predicts that triparental sex dominates biparental sex, so the latter should not be observed, contrary to fact.

Keywords: Biparental sex; Triparental sex; Purpose of sex; Twofold cost of sex; Deleterious mutations.

1. Introduction

Understanding the purpose of sex is one of the most important problems in evolutionary biology (Otto and Lenormand, 2002; Rice, 2002). One explanation as to why it remains unresolved is as follows.

One of the great struggles in the evolution-of-sex literature is to find a prediction that is truly discriminating between hypotheses (Hurst and Peck, 1996).

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We wish to suggest a candidate for such a prediction based upon the following remarkable, yet unexploited, empirical regularity. *Each sexually produced offspring of any known eukaryotic species is produced from the genetic material of precisely two individuals. That is, sex is always biparental.*

A complete theory of sex, therefore, must explain not only why genetic mixing is sufficiently beneficial that biparental sex overcomes the twofold cost of males it suffers relative to asexual reproduction (Maynard Smith, 1978), it must also predict that among all possible sexual systems – asexual, biparental, triparental, etc. – biparental sex will come to dominate the population.

Insisting that a theory of sex predict the evolutionary success of biparental sex over all other sexual systems places stringent demands on the theory. On the one hand, genetic mixing must be sufficiently beneficial to overcome the twofold cost of biparental sex over asexual reproduction, yet 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 or quadriparental sex, etc. A viable theory of sex, therefore, must strike a delicate balance – genetic mixing must be advantageous, but not too advantageous. The latter demand – that sex not be too advantageous – has been overlooked in the purpose-of-sex literature. Yet, it can furnish a powerful test of a hypothesis.

Why is it that little or no attention has been paid to whether a theory of biparental sex inadvertently confers an advantage to, say, triparental sex? Perhaps it is because one is tempted to dismiss triparental sex altogether on the grounds that the associated costs — be they the cost of unproductive males, mating co-

ordination costs, or the cost of developing the requisite genetic machinery — are prohibitive. But, insofar as such arguments have been provided at all, they are unpersuasive. For example, 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 idea that consideration of biological systems that are *not* observed in nature can provide a deeper understanding of the systems that *are* observed in nature is not new. Such an approach to biology has a long tradition and is eloquently promoted by R.A. Fisher (1930, p. ix) who, on the separate issue of the number of mating compatibility classes, had this to say.

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?

As an example of the power of this approach, we consider whether the mutational deterministic (MD) hypothesis (Kondrashov, 1982, 1988) for the maintenance of biparental sex correctly predicts the absence of triparental sex.

Under the MD hypothesis, we find that triparental sex has a net 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. That is, in environments conducive to

biparental sex, the MD hypothesis predicts even greater evolutionary success to triparental sex. The MD hypothesis therefore incorrectly predicts that biparental sex should not be observed.

Thus, a theory's prediction about the sexual system that will come to dominate the population can provide a powerful test of the theory. Whether it is "truly discriminating between hypotheses" remains an important open question that is explored in the discussion section.

2. Triparental sex

Triparental sex will be said to occur when each cell of an offspring contains genetic material from three parents – one mother and two fathers, perhaps. For example, each parent might contribute an equal share of the offspring's genes. But this is just one possibility. Another possibility is that the mother contributes one-half of the offspring's genes and the two fathers each contribute one-quarter. In theory, there are infinitely many triparental sexual systems.

One might attempt to explain the absence of triparental sex by suggesting that it is too costly. We next discuss why several such cost-based arguments are unconvincing.

First, there is the obstacle of developing the requisite genetic machinery for combining the genetic material of more than two parents. Unlike the case of eukaryotes, where triparental sex has never been observed, in the case of bacteriophages – bacterial viruses – triparental sex is not unusual. Indeed, the DNA of a bacteriophage can be a combination of the DNA of two, three or more par-

ents (Stent, 1963). The existence of such systems of reproduction suggests that there is, in principle, no insuperable obstacle to developing the requisite genetic machinery for multiparental sex more generally.

Second, one might argue that the costs of coordinating the mating of three individuals over just two outweigh the potential benefits (Power, 1976). To be taken seriously, such an argument must carefully consider the additional benefits and coordination costs incurred not only in the transition from biparental to triparental sex, but also in the transition from asexual reproduction to biparental sex. A serious difficulty for any such argument is that while there are clearly significant additional coordination costs involved in the transition from asexual to biparental sex – e.g., a technology for locating mates must be developed and maintained – the ample empirical evidence for sperm competition (Parker, 1970) implies that the additional coordination cost of triparental sex over biparental sex is negligible for a large number of species. Indeed, as the following quote explains, the prevalence of sperm competition implies that biparental mating behavior routinely brings together, within a single female, genetic material from multiple males.

A common assumption about reproduction is that the spermatozoa in the vicinity of ova around the time of fertilization are from a single male. However, for a wide range of organisms, both internal and external fertilizers, this assumption is almost certainly wrong. It is wrong because among internal fertilizers, females typically copulate with more than one male during a single reproductive cycle, and among

externally fertilizing animals, often several males simultaneously release spermatozoa near a spawning female. When the ejaculates from two or more males compete to fertilize the ova of a particular female, the process is referred to as sperm competition. Sperm competition is virtually ubiquitous and its biological consequences are considerable. (Birkhead (1998))

Sperm competition occurs, for example, in birds (Goetz et. al., 2003; Parrott, 2005), ants and bees (Hölldobler and Wilson, 1994), shrimp (Bilodeau et. al., 2004), snails (Evanno et. al., 2005), snakes (Garner et. al., 2002), tortoise (Roques et. al., 2004), and fruit-flies (Bressac and Hauscheteck-Jungen, 1996). In all these cases, which are by no means exhaustive, triparental sex — e.g., where the sperm of two distinct males fertilize a single egg — would entail negligible additional coordination costs over biparental sex.

Third, there is the “cost of sex.” A biparental sexual population with a one to one ratio of unproductive males to females produces half as many offspring as an equally-sized asexual population (Maynard Smith, 1978). One might then expect triparental sex – involving two unproductive males and one female – to display a threefold cost of males relative to asexual reproduction. But, in fact, the cost of males depends upon which of the infinitely many triparental systems is in force. There is one particular triparental system that, on the one hand, generates more genetic mixing than biparental sex, yet, on the other hand, entails *no additional cost of males* relative to biparental sex. It is the system in which the offspring

receives one-quarter of its genes from each its two fathers, and one-half of its genes from its mother, a system that we will henceforth refer to as $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ triparental sex, or simply $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ sex. We now explain why $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ sex entails the same twofold cost of males as biparental sex.

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 (Fisher, 1930). 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 – there is no additional cost of males over biparental sex.

Summing up, (i) developing genetic machinery may not be an insuperable barrier to triparental sex, (ii) the additional coordination costs to triparental sex over and above those of biparental sex are negligible in many species, and (iii) $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ sex entails no additional cost of males relative to biparental sex.

Our next step is to compare the fitness – net of costs – of triparental sex

versus biparental sex under the MD hypothesis. In the standard MD model, with the exception of the cost of unproductive males, *all* costs of biparental sex – including coordination costs – are ignored. To provide an appropriate comparison, coordination costs will therefore be ignored here as well. However, it should be noted that this will bias our results *against* triparental sex if – see (ii) above – the cost of coordinating biparental sex over asexual reproduction is large relative to the additional cost of coordinating triparental sex over biparental sex, something that seems likely to hold in nature. This point is discussed further following the MD analysis below.

Thus, in the following section, we compare the fitnesses of biparental and triparental populations under the MD hypothesis maintaining the literature’s standard assumption of zero mating coordination costs. Despite the possible bias against triparental sex that this procedure may introduce, it is shown that $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ triparental sex has a uniform fitness advantage over biparental sex. The MD hypothesis is therefore unable to explain the presence of biparental sex and the absence of triparental sex.

What about the fitness consequences of $\frac{1}{3}$ - $\frac{1}{3}$ - $\frac{1}{3}$ triparental sex, where each parent contributes equally to the offspring? This sexual system provides even more mixing than $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ sex, and can be shown to yield an even greater *gross* increase in fitness under the MD hypothesis. However, Fisher’s argument establishes that $\frac{1}{3}$ - $\frac{1}{3}$ - $\frac{1}{3}$ sex entails a threefold cost of males over asexual reproduction. On balance, for all parameter values considered here the population grows faster under $\frac{1}{4}$ - $\frac{1}{4}$ - $\frac{1}{2}$ sex than under $\frac{1}{3}$ - $\frac{1}{3}$ - $\frac{1}{3}$ sex.

3. The mutational deterministic hypothesis

According to the mutational deterministic hypothesis (Kondrashov, 1982, 1988), sex is advantageous even in large populations because it permits a species to more efficiently eliminate harmful mutations by increasing the variance of their distribution, thereby increasing the number of mutational deaths per individual death. The first theory of this kind is due to Muller, but relies upon a finite population where sex can reverse the otherwise steady accumulation of mutations (Muller, 1932, 1964).

Kondrashov (1982) assumes the following. 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 u , 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 their survival.

Kondrashov's analysis of a large 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

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

Now, because it is assumed that 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,

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

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.

Let us 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 $m' + n' = i$. Analogously to Kondrashov, it is assumed that the three parents have no more than one mutation in total at each locus. Consider a locus where there is a mutation. Saying that sex is $\frac{1}{4}-\frac{1}{4}-\frac{1}{2}$ means that if the mutation belongs to the mother it is inherited with probability one-half, and if it belongs to one of the fathers it is inherited with probability one-quarter. Hence, because there is no linkage, 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 addi-

tional 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 Kondrashov (1982) and Howard (1994).

u	$K = 5$	$K = 20$	$K = 60$	$K = 80$	α
1	2.1	1.0	0.4	0.3	∞
	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	∞
	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	∞
	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	∞
	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	∞
	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	∞
	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, (u, K, α) . Maintaining Kondrashov's assumption that the only cost of sex is the cost of males, there is no additional 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.

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 sufficiently high 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 (Kondrashov, 1988; Charlesworth, 1990; and Howard, 1994)— 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 (Keightley and Eyre-Walker, 2000).

This also shows how a large but ignored coordination cost to biparental sex over asexual reproduction, together with a small additional cost to triparental sex would bias our results. A large coordination cost from asexual to biparental sex would *increase* the mutation rate at which biparental sex dominates asexual reproduction – from 1-2 mutations per genome per generation to, possibly, 3-4 – while a small coordination cost from biparental to triparental sex would have little impact on our relative fitness figures in Table 1. Thus, the entries in Table 1 would be essentially unchanged, but more of them would be marked with an asterisk – e.g. only mutation rates above 3 or 4, say, might be consistent with biparental sex dominating asexual reproduction. But for these high mutation rates, triparental sex has a substantial advantage over biparental sex and the case against the MD hypothesis would be even stronger.

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

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.

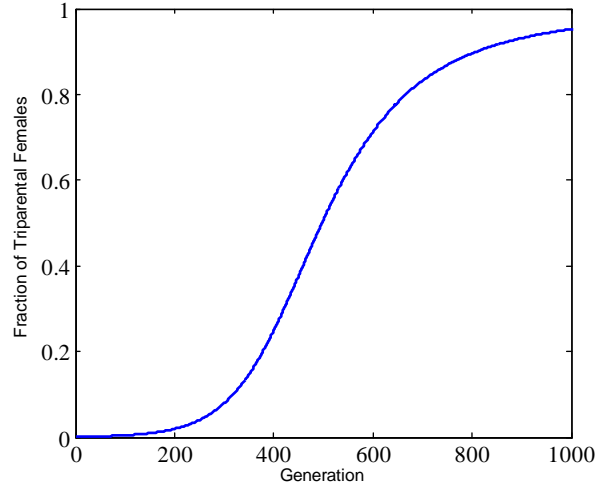


Figure 1: $f = 0.001$, $u = 3$, $K = 20$, $\alpha = 2$

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.

4. Discussion.

There are two major classes of theories on the maintenance of sex, those based upon the purging of deleterious mutations, and those based upon adaptation to the environment.

In the deleterious mutation model analyzed here, the post-sex variance of the distribution of mutations is the average of the pre-sex mean and variance. There-

fore if, in a biparental-sex equilibrium, the post-sex mean number of mutations exceeds its variance (as it does for all parameter values considered), additional (pre-selection) sex *increases* the variance. Combined with the tendency of selection exhibiting synergistic epistasis to favor mean-preserving increases in variance, this explains why triparental sex dominates biparental sex for all parameter values considered.

Because many deleterious mutation models incorporate synergistic epistasis (Charlesworth, 1990; Howard 1994; Kondrashov, 1982, 1988), triparental sex may be expected to dominate biparental sex in these models as well. A possible exception arises in a model of mutational meltdown in finite populations with zero epistasis (Lynch and Gabriel, 1990). Because reducing epistasis to zero eliminates a potential advantage of triparental sex over biparental sex, such a model may be consistent with the absence of triparental sex.

We next consider three subclasses of theories based upon adaptation to the environment. In directional selection models, sexual reproduction increases genetic and phenotypic variance and can permit a species to better track the optimum phenotype in a changing environment (Charlesworth, 1976; Crow, 1992; Maynard Smith, 1980, 1988; Waxman and Peck, 1999). When conditions are favorable for biparental sex, additional genetic mixing – as would occur under triparental sex – may increase genetic variance further and be even more favored. If so, directional selection hypotheses would fail to predict the absence of triparental sex.

Host-parasite coevolution models can yield an advantage to biparental sex when selection effects are sufficiently strong (Hamilton, 1980; Hamilton et. al.,

1990; Jaenike, 1978; Otto and Nuismer, 2004; Peters and Lively, 1999). Whether triparental sex would appreciably increase this advantage is unclear and must await further study.

A third subclass of environmental models are those based upon the Hill-Robertson effect (Barton and Otto, 2005; Felsenstein, 1974; Felsenstein and Yokoyama, 1976; Hill and Robertson, 1966; Martin et. al., 2006; Otto and Barton, 1997, 2001; Iles et. al., 2003). In these models, sex and recombination permit the species to improve faster when the fixation effect of selection without sex (or with low levels of recombination) leads to negative linkage disequilibrium. Importantly, this effect is present even under zero epistasis (Otto and Barton, 1997). Once again, because zero epistasis eliminates a potential source of advantage of triparental sex over biparental sex, hypotheses based upon the Hill-Robertson effect with zero epistasis may be consistent with the absence of triparental sex.

Finally, there are hybrid models involving both deleterious mutation effects and coevolution effects (Howard and Lively, 1994, 1998; West et. al. 1999). Because these hybrid models can explain biparental sex under a wider range of parameter values than any of the individual models taken separately, it would be of interest to compare triparental and biparental sex in such hybrids.

We have shown here that under the MD hypothesis, triparental sex always dominates biparental sex, that the advantage is significant at modest genomic mutation rates, and that higher mutation rates only serve to increase this advantage. With all three options – asexual, biparental, triparental – available, fitness would be highest either under asexual reproduction or under triparental sex. Ac-

cordingly, biparental sex should not be observed, contrary to fact. Thus the MD hypothesis fails to predict the absence of triparental sex.

Is the prediction that sexual reproduction is always biparental, and not triparental or more, “truly discriminating among hypotheses?” While a definitive answer awaits further study, it is suggested here that theories relying upon synergistic epistasis are less likely to be consistent with the prediction than those permitting zero epistasis.

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