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Why are there only two sexes?

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SUMMARY

Populations of most isogamous protists have gametes that belong to one of only two mating-types (alias sexes). That this should be so is paradoxical for, if there is any cost involved in the finding of a mate, then a gamete of a third mating-type would, at the point of invasion, be able to mate with the first gamete it encounters, hence suffering the minimum possible costs. The expectation is hence that the number of mating-types in most isogamous species should tend towards infinity. By the same logic, two mating-types is the least expected state. A demonstration of the evolution from three to two sexes, under the condition of costs to mate-finding, has yet to be provided. Here I show by a dynamic analysis that, if species with two mating-types coordinate uniparental inheritance of cytoplasmic genes more efficiently than do those with three, then, assuming the costs to mate finding are not too high, evolution from three to two sexes is expected as a response to the invasion of a costly selfish cytoplasmic factor that disrupts the normal pattern of inheritance. There exists also a limited domain in parameter space (in which costs to mate finding are moderate), in which collapse from four mating-types to three is possible, but the collapse from three to two is not. If costs to not finding a mate are high then it is expected that gametic fusion should be abandoned for a system in which nuclei are exchanged but cytoplasm is not.

1. INTRODUCTION

‘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 sexes are, in fact always two?’ R. A. Fisher (1930).

Populations of isogamous protists, of which the alga *Chlamydomonas* would be a good example, are typically divided into two mating-types. Cells that are + type can mate only with those that are – type and vice versa. That species should ever have evolved two mating-types when initially there were none, is as paradoxical as is the fact that when mating-types are present they are typically binary. Consider a system in which only two gametes must meet for zygote formation. Consider also then that there were no mating-types. If this was true, a gamete could mate with any other gamete. If however there are two mating-types then any gamete can mate with only half the population. Hence, the transition from having no mating-types to having two is one in which the problem of finding a mate becomes harder and is hence problematic.

Now consider the situation in which there are two mating-types. A gamete with a novel third type will be able to mate with all other gametes when it initially appears in the population. Assuming there to be some cost to the finding of mates, one would hence expect that such a mutant should easily invade. The same is true for the invasion of any novel mutant into a population with more than two mating-types. It is therefore to be expected that either there should be

zero mating-types or, if for whatever reason mating-types have evolved, that the number of mating-types should tend towards infinity (Iwasa & Sasaki 1987). Two sexes is the least expected condition. It is therefore remarkable that so many organisms have two sexes.

Why then did mating-types evolve in the first place (the transition from zero to two) and why do so many organisms have only two sexes/mating-types? A variety of answers to the former paradox have been proposed (Hoekstra 1987; Hoekstra *et al.* 1991). Avoidance of inbreeding is often considered an important possible force. An alternative that receives some empirical support (Hurst & Hamilton 1992; Hurst 1995) is that mating-types evolve in response to selfish cytoplasmic factors as a means to coordinate organelle inheritance (Hoekstra 1987; Hurst & Hamilton 1992; Hutson & Law 1993). This model is consistent with numerous features of the structure and function of the best described mating-type locus, that of *Chlamydomonas* (Armbrust *et al.* 1993; Hurst 1995), not least of which is that the alleles coordinate both mating preferences and cytoplasmic inheritance. In addition, this model is consistent with an absence of incompatibility types associated with biparental inheritance in somatic cell fusions and the absence of mating-types in species in which syngamy does not involve fusion of cells with organelles (reviewed in Hurst 1995).

Based on a parallel logic, a theory has been verbally outlined as to why a species with three mating-types might evolve into one with only two (Hurst & Hamilton 1992; Hurst 1995). Here I provide a formal analysis of the problem and show that if species with more than three mating-types are more vulnerable to

selfish cytoplasmic factors than are those with two, then a three mating-type species may deterministically return to having two, even if there are costs to mate-finding.

Both the previous discussion of the problem (Iwasa & Sasaki 1987) and the analysis presented here consider only one of the three possible meanings of what a species with three mating-types would be like. We assume that mating-types function such that only two gametes must meet for zygote formation and that they need only be of different type for sex to occur. Alternatively, however, one could imagine a species in which, again only two gametes are required, but a gamete of type-1 could mate only with type-2 and not type-3, while type-3 could mate only with type-2 and not type-1 (Bull & Pease 1989). On the average, mate finding is not as easy as it might be in such a system (Bull & Pease 1989). That such systems are not found suggests that the pressure to ease the finding of a mate is a realistic selective pressure on the form of mating-types (Bull & Pease 1989). Finally, one might envisage a system of three mating-types in which three gametes, one of each type, must come together for zygote formation. This would make mate finding especially difficult and it is again probably for this reason that no such system exists (Power 1976) (although, to stretch a point, one might argue that some viral systems requiring more than two independent components are comparable).

2. THE MODEL

Consider then a population of haploid unicellular isogamous protists in which there are three mating-types (numbered 1, 2, 3) determined by one of three alleles at the mating-type locus. An individual of any given mating-type can mate with any gamete of different type. In any pair-wise mating the inheritance of cytoplasmic factors needs to be coordinated (Grun 1976; Cosmides & Tooby 1981; Hoekstra 1990; Hurst 1990; Hastings 1992; Hurst & Hamilton 1992; Law & Hutson 1992). Typically this means the enforcement of uniparental inheritance. Let us suppose that under normal conditions a hierarchy exists for the control of cytoplasmic gene inheritance: type-3's mitochondria are always inherited, type-1's are never inherited. In a type-2/type-1 mating then, those of type-2 are inherited and in a type-2/type-3 mating, those of type-3 are inherited. A precedent for such a hierarchy has been described (Kawano & Kuroiwa 1989; Meland *et al.* 1991).

Now consider a selfish cytoplasmic element that forces biparental inheritance. Such unusual selfish elements have been described in species with more than two mating-types (Kawano *et al.* 1991). By virtue of the nature of the hierarchy, I shall assume that the selfish cytoplasmic factor can gain most when the two cells fusing are closely aligned in the hierarchy (i.e. in type-1/type-2 matings and type-2/type-3 matings). In the matings, the selfish cytoplasmic factor, if in the lower but not the higher member of the hierarchy, is

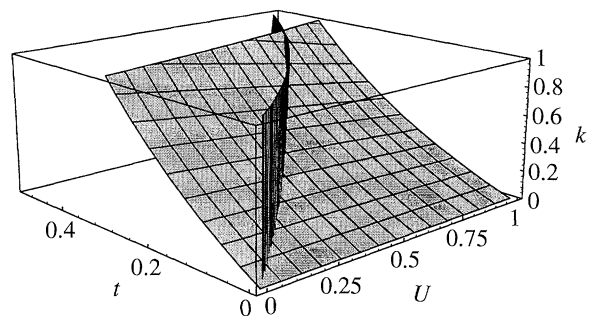


Figure 1. Approximations for the invasion conditions for the selfish element and for the novel mating type. The invasion conditions for the selfish element are plotted below as the sheet rising from the U -axis as t increases. The value of k possessed by the selfish element must lie above the space defined by the sheet ($k > 1$ is impossible). The invasion conditions of the novel mating type, for the condition that the selfish element exists in 90% of individuals, are plotted as the vertical sheet (note for high values of t , $m = 0.9$ may not be achievable). For invasion, the parameters values must sit to the left of the sheet. This hence shows that there exists a relatively broad space in which the selfish element can invade and a sub-space within which, even with relatively high costs to mate-finding, the novel mating type can invade. It is here assumed that there is no leakage, i.e. $\alpha = 1$.

transmitted at a rate k to the progeny (for simplicity I assume progeny cells are homoplasmic). If in the higher member of the hierarchy, uniparental inheritance is unaffected. I shall start by assuming that matings between type-3 and type-1 cells always result in the inheritance of type-3's cytoplasmic constituents.

If a progeny cell inherits the selfish factor then it suffers a cost, t . I shall also assume that gametes meet at random. If two gametes are of the same mating-type then they do not fuse and suffer some cost, U , for so doing. This is, in effect, the cost of mate-finding. If the frequency of mating-types 1, 2 and 3 are p , q and r respectively, and ps is the frequency of type-1 cells with the selfish element, and pw that with the wild-type ($ps + pw = p$) (likewise qs , qw etc.), then the following recursions, describing the dynamics of each class of mating-type, can be deduced (see table 1):

$$pw' = \frac{[pw((pw + ps)(1 - U) + qw + rw) + ps(qw(1 - k) + rw)]}{\bar{W}}$$

$$ps' = \frac{[(1 - t)((ps((pw + ps)(1 - U) + qs + rs + qwk)) + pw(qs + rs))]}{\bar{W}}$$

$$qw' = \frac{[qw((qw + qs)(1 - U) + pw + rw + ps(1 - k)) + qsrw(1 - k)]}{\bar{W}}$$

$$qs' = \frac{[(1 - t)(qs((qw + qs)(1 - U) + ps + rs + pw + rwk) + qw(psk + rs))]}{\bar{W}}$$

$$rw' = \frac{[rw((rw + rs)(1 - U) + pw + ps + qw + qs(1 - k))]}{\bar{W}}$$

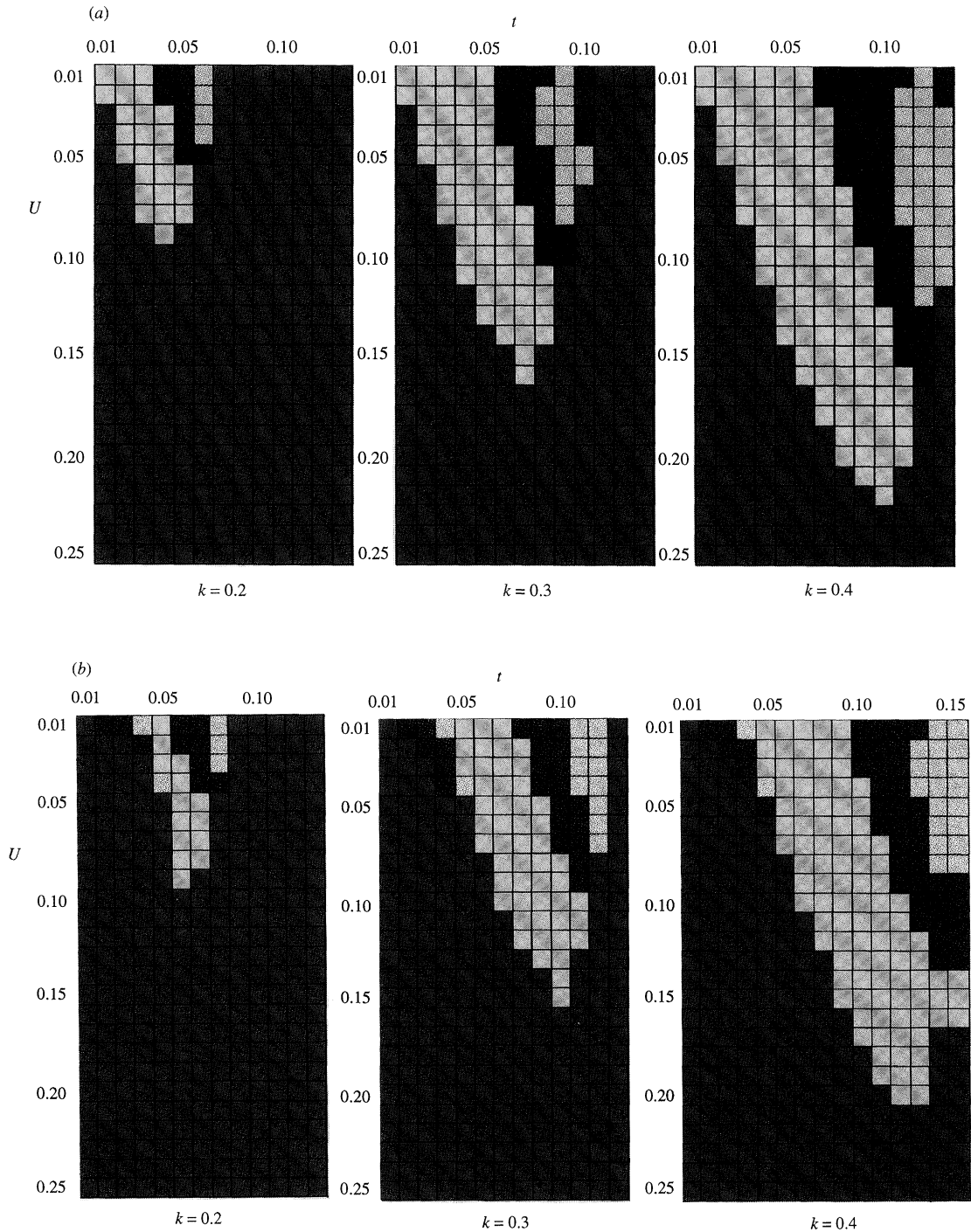


Figure 2. The equilibrium number of alleles at the mating-type locus after invasion by a selfish cytoplasmic genome and the subsequent invasion the type-(2+3) allele. Those cases where the type-(2+3) allele could not invade are shown in dark grey. When invasion is possible three equilibrium solutions are found: (a) two alleles persist, i.e. (type-(2+3) and type-1), (shown in light grey); (b) the three original mating-type alleles persist (shown in black); and (c) all four alleles persist (shown in white). The first row of three values of k are done for the condition of no leakage ($\alpha = 1$). The second row is for the condition $\alpha = 0.9$. Note that as leakage increases so the number of simulations giving two sexes goes down (see also figure 3). Note also that as leakage increases so the invasion of the selfish cytotype becomes easier and the distribution moves to the right while shrinking. These outcomes are found through simulation. Simulation started with types 1, 2 and 3 at equal frequency (0.33) and a selfish element is introduced in a member of type-1 at frequency 0.005. vw is also set to 0.005. If all gene frequencies do not change by more than 10^{-7} then the simulation is stopped and assumed to be at equilibrium. If the frequency of any of the seven gamete types goes below 10^{-6} then the frequency of this type is set to zero.

Table 1. *The frequencies of encounter and the proportion of resulting cells from each meeting along with their fitness components*

(Mt 1, 2 and 3 are mating types 1, 2 and 3, W indicates wild-type cytotype, S indicates selfish cytotype. The novel mating-type (Mt-(2+3)) also exists either with the wild-type cytotype or the selfish one. If two cells of incompatible type meet (e.g. type-1 with type-1, type 2 with type-(2+3) etc.) then mating does not occur and the two cells part suffering a cost of not mating (1-U) and any cost associated with the cytotype they possess. These cells may be thought of as asexual progeny. If the cells are compatible then mating occurs and sexual progeny are produced. These sexual encounters also provide the conditions for the spread of the selfish cytotype. In type-1/type-2 and type-2/type-3 matings the selfish cytotype is transmitted at rate *k* to progeny if the lower member of the hierarchy bears it, but the higher does not. Otherwise in these matings the higher member's cytotype is inherited exclusively. In matings between individuals more distant in the hierarchy (i.e. type-1/type-3 and type-1/type-(2+3)) a small leakage of the selfish cytotype may occur if the lower party bears it. Most progeny (proportion α) will hence bear the cytotype of the higher member of the hierarchy. From this table a general form of the recursion can be deduced:

$$\begin{aligned}
 pw' &= \frac{[pw((pw+ps)(1-U)+qw+rw+vw)+ps(qw(1-k)+\alpha rw+\alpha vw)]}{\bar{W}}, \quad ps' = \frac{[(1-t)(ps((pw+ps)(1-U)+gs+(1-\alpha)rw+rs+qwk+vs+(1-\alpha)vw))+pw(qs+rs+vs)]}{\bar{W}} \\
 qw' &= \frac{[qw((qw+qs+vs+vw)(1-U)+pw+rw+ps(1-k))+qsrw(1-k)]}{\bar{W}}, \quad qs' = \frac{[(1-t)(qs((qw+qs+vs+vw)(1-U)+ps+rs+pw+rwk)+qw(psk+rs))]}{\bar{W}} \\
 rw' &= \frac{[rw((rw+rs+vs+vw)(1-U)+pw+\alpha ps+qw+qs(1-k))]}{\bar{W}}, \quad rs' = \frac{[(1-t)(rs((rw+rs+vs+vw)(1-U)+ps+qs+pw+qw)+(1-\alpha)rups+ruqsk)]}{\bar{W}} \\
 vw' &= \frac{[vw((rw+rs+qw+qs+vw+vs)(1-U)+pw+\alpha ps)]}{\bar{W}}, \quad vs' = \frac{[(1-t)(vs((rw+rs+qw+qs+vw+vs)(1-U)+pw+ps)+(1-\alpha)psvw)]}{\bar{W}}
 \end{aligned}$$

where \bar{W} is the sum of the numerators. To obtain the first set of recursions provided in the text (the case where there is no new mating type and no leakage) allow $\alpha = 1$, $vs = vw = 0$. To obtain the second set (no leakage with the novel allele) allow $\alpha = 1$ and $vs = 0$, $vw = v_s$.

		proportion of 'progeny' and their fitnesses							
mating	frequency	Mt-1 W	Mt-1 S	Mt-2 W	Mt-2 S	Mt-3 W	Mt-3 S	Mt-(2+3) W	Mt-(2+3) S
Mt-1 W × Mt-1 W	pw^2	1-U	—	—	—	—	—	—	—
Mt-1 W × Mt-1 S	2 $pw ps$	0.5 (1-U)	0.5 (1-U) (1-t)	—	—	—	—	—	—
Mt-1 W × Mt-2 W	2 $pw qw$	0.5	—	0.5	—	—	—	—	—
Mt-1 W × Mt-2 S	2 $pw qs$	—	0.5 (1-t)	—	0.5 (1-t)	—	—	—	—
Mt-1 W × Mt-3 W	2 $pw rw$	0.5	—	—	—	0.5	—	—	—
Mt-1 W × Mt-3 S	2 $pw rs$	—	0.5 (1-t)	—	—	—	0.5 (1-t)	—	—
Mt-1 W × Mt-(2+3) W	2 $pw vw$	0.5	—	—	—	—	—	0.5	—
Mt-1 W × Mt-(2+3) S	2 $pw vs$	—	0.5 (1-t)	—	—	—	—	—	0.5 (1-t)
Mt-1 S × Mt-1 S	ps^2	—	(1-U) (1-t)	—	—	—	—	—	—
Mt-1 S × Mt-2 W	w $ps qw$	0.5 (1-k)	0.5 k (1-t)	0.5 (1-k)	0.5 k (1-t)	—	—	—	—
Mt-1 S × Mt-2 S	2 $ps qs$	—	0.5 (1-t)	—	0.5 (1-t)	—	—	—	—
Mt-1 S × Mt-3 W	2 $ps rw$	0.5 α	0.5 (1- α) (1-t)	—	—	0.5 α	0.5 (1- α) (1-t)	—	—
Mt-1 S × Mt-3 S	2 $ps rs$	—	0.5 (1-t)	—	—	—	0.5 (1-t)	—	—
Mt-1 S × Mt-(2+3) W	2 $ps vw$	0.5 α	0.5 (1- α) (1-t)	—	—	—	—	0.5 α	0.5 (1- α) (1-t)
Mt-1 S × Mt-(2+3) S	2 $ps vs$	—	0.5 (1-t)	—	—	—	—	—	0.5 (1-t)
Mt-2 W × Mt-2 W	qw^2	—	—	1-U	—	—	—	—	—
Mt-2 W × Mt-2 S	2 $qw qs$	—	—	0.5 (1-U)	0.5 (1-U) (1-t)	—	—	—	—
Mt-2 W × Mt-3 W	2 $qw rw$	—	—	0.5	—	0.5	—	—	—
Mt-2 W × Mt-3 S	2 $qw rs$	—	—	—	0.5 (1-t)	—	—	—	—

Mt-2 W × Mt-(2+3) W	0.5 (1-U)	0.5 (1-U) (1-U)	0.5 (1-U)	0.5 (1-U) (1-U)
Mt-2 W × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-U)	0.5 (1-U)	0.5 (1-U) (1-U)
Mt-2 S × Mt-2 S	0.5 (1-k)	0.5 (1-k)	0.5 (1-k)	0.5 (1-k)
Mt-2 S × Mt-3 W	0.5 (1-U) (1-t)	0.5 k (1-t)	0.5 (1-k)	0.5 k (1-t)
Mt-2 S × Mt-3 S	0.5 (1-t)	0.5 (1-t)	0.5 (1-t)	0.5 (1-t)
Mt-2 S × Mt-(2+3) W	0.5 (1-U) (1-t)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-2 S × Mt-(2+3) S	0.5 (1-U) (1-t)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 W × Mt-3 W	1-U	1-U	1-U	1-U
Mt-3 W × Mt-3 S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 W × Mt-(2+3) W	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 W × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 S × Mt-3 S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 S × Mt-(2+3) W	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-3 S × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-(2+3) W × Mt-(2+3) W	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-(2+3) W × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-(2+3) S × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)
Mt-(2+3) S × Mt-(2+3) S	0.5 (1-U)	0.5 (1-U) (1-t)	0.5 (1-U)	0.5 (1-U) (1-t)

$$rs' = \frac{[(1-t)(rs((rw+rs)(1-U)+ps+qs+pw+qw) + rwqsk)]}{\bar{W}}$$

where \bar{W} is the sum of the numerators.

The invasion conditions for the selfish element can be approximated by assuming that the mutant is equally likely to initially occur in each of the three mating-types ($ps = qs = rs$). The conditions are then found by solving $dm'/dm > 1$ at $m = 0$ and $pw = qw = rw = 1/3$ where $m = ps + qs + rs$ (i.e. the frequency of the selfish gene). This reveals that for invasion that:

$$k > \frac{3t(3-U)}{4(1-t)}$$

must be satisfied. This is plotted in figure 1. Note that as the cost associated with the element goes up, so the level of transmission (k) must go up for invasion to be possible. As a proportion of all costs, for given t , the effect of the cytoplasmic element on mean fitness, goes down as U goes up. Hence, for increasing U and given t , the minimum k required tends go down (except when $t = 0$). Simulation allowed assessment of the fate of the selfish cytoplasmic factor. It is found that invasion may be followed by fixation, or by a stable polymorphism if t is relatively high.

Consider that the selfish mutant has yet to go to fixation. Consider then what happens if a mutant at the mating-type locus should appear that, perhaps because of some rare recombination event, has in tight linkage both the mating-type-2 allele and the type-3 allele. This I shall refer to as type-(2+3). Such a cell can mate only with type-1 gametes. I shall start by assuming that when such mating occurs, type-(2+3)'s cytoplasmic genes are inherited, regardless of the presence or absence of the selfish element (as in type-1/type-3 matings). This new mating-type hence remains with the cytotype with which it is initially associated (cf. Hoekstra 1990; Hastings 1992). If associated with the selfish type it can hence be expected never to invade. I thus initially consider only the dynamics of what happens when the type-(2+3) mutant (at frequency v) is associated with the wild-type cytotype. The recursions (derived from table 1) after this new mating-type is incorporated become:

$$pw' = \frac{[pw((pw+ps)(1-U)+qw+rw+v) + ps(qw(1-k)+rw+v)]}{\bar{W}}$$

$$ps' = \frac{[(1-t)((ps((pw+ps)(1-U)+qs+rs+qwk)) + pw(qs+rs)))]}{\bar{W}}$$

$$qw' = \frac{[qw((qw+qs+v)(1-U)+pw+rw+ps(1-k)) + qsrw(1-k)]}{\bar{W}}$$

$$qs' = \frac{[(1-t)(qs((qw+qs+v)(1-U)+ps+rs+pw+rwk) + qw(psk+rs)))]}{\bar{W}}$$

$$rw' = \frac{[rw((rw + rs + v)(1 - U) + pw + ps + qw + qs(1 - k))]}{\bar{W}}$$

$$rs' = \frac{[(1 - t)(rs((rw + rs + v)(1 - U) + ps + qs + pw + qw) + rwqsk)]}{\bar{W}}$$

$$v' = \frac{[v((rw + rs + qw + qs + v)(1 - U) + pw + ps)]}{\bar{W}}$$

where \bar{W} is the sum of the numerators.

If the population is lacking the selfish element, the new mutant will be lost as it suffers higher than average costs of mate-finding (assuming $U > 0$). As, however, the rare type-(2+3) mutant is initially associated with the relatively fit cytotype, if the population is afflicted with the selfish cytoplasmic factor, then the type-(2+3) allele can sometimes spread within the population, despite the costs of mate-finding. This is because it always stays associated with (i.e. in linkage disequilibrium with) the relatively fit cytotype. The invasion conditions of the novel mating-type can be approximated by solving $dv'/dv > 1$ for the condition that $ps = qs = rs = m/3$ and $pw = qw = rw = (1 - m)/3$. This reveals that for the novel mating-type to invade:

$$U < \frac{mt(9 + 4k - 4mk)}{3(1 + mt)}$$

must hold (see figure 1). When the novel mating-type is infinitely rare then for it to invade, the selfish genome must be adequately common, the costs to mate finding must not be excessively high while, conversely, the costs to having the selfish genome must not be too low. Similarly however, as the cost to having the selfish element (t) becomes too large, so the selfish element cannot invade and hence neither can the type-(2+3) allele. As k goes up so the invasion of the selfish cytotype becomes easier and hence the parameter space consistent with invasion of the type-(2+3) mating-type also expands.

The fate of this new genotype can be explored through simulation (figure 2). Three equilibrium solutions are found.

1. Two alleles persist, i.e. (type-(2+3) and type-1): the mutant mating-type invades, eliminates both type-2 and type-3 and then also eliminates the selfish cytoplasmic factor (which typically goes almost instantaneously to high frequencies).

2. Three alleles persist: after the type-(2+3) allele invades, it purges the population of the selfish genome, but does so before the extinction of alleles 2 and 3. These two re-invade and eliminate type-(2+3), hence the three original mating-type alleles persist free from the selfish element.

3. All four alleles persist, in which case, so does the selfish element at some low frequency. This typically occurs if the selfish factor can only just invade (i.e. if t is at its upper limits and U is low).

This boundary between the position at which the type-2 and type-3 alleles are not eliminated before selfish element elimination and that at which they are,

is sensitive to alterations in k and t as well as U (see figure 2). It is to be expected that most populations in which the k and t parameters are such that two sexes are not achieved, will eventually be forced back to two mating-types through the force of a selfish element of appropriate cost (t) and/or gain (k).

3. THE EFFECT OF LEAKAGE

Above it was assumed that in type-1/type-3 and type-1/ type-(2+3) matings, the selfish cytotype is never inherited if present in the lower but not the higher member of the hierarchy. As a consequence tight linkage disequilibrium between the novel mating-type and the wild-type cytotype can be maintained. This assumption can be relaxed, what might be considered 'leakage'. When this is done it is necessary to expand the recursions to allow in the possibility of a type-(2+3) that is associated with the selfish cytotype (at frequency vs , the type-(2+3) with the wild-type cytotype now being at frequency vw) (see table 1). In matings between type-1 and type-3 cells and those between type-1 and type-(2+3), if type-1 has the mutant factor but the mate does not, then a large proportion, α inherit the wild-type cytotype whereas in a proportion $1 - \alpha$ leakage occurs and they inherit the selfish mutant.

With leakage, linkage disequilibrium between type-(2+3) and the relatively fit cytotype can decay. As type-(2+3) cells infected with the selfish cytotype have the worst of both worlds (they find mate finding difficult and suffer the cost of having the selfish cytoplasmic factor) one would expect that leakage would inhibit evolution from two to three mating-types. This is confirmed by simulation (figure 3). Interestingly however, whereas leakage is generally inhibitory to the process, it is not inhibitory to the

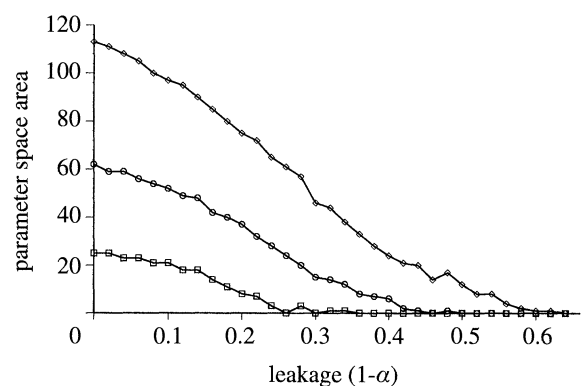


Figure 3. The number of simulations giving a return to two sexes against the degree of leakage ($1 - \alpha$) for three different values of transmission (k). The square points are for $k = 0.2$, circles for $k = 0.3$ and diamonds for $k = 0.4$. Each point represents the outcome of 1050 simulations: every point in parameter space for values of U from 0.01 to 0.3 and for t from 0.01 to 0.35 at increments of 0.01 (outside this space invasion is never possible for $k < 0.4$). The number of simulations giving two sexes is hence an area in parameter space equivalent to the number of squares in light grey in figure 2.

evolution of two mating-types at all parameter values (see figure 2). At high values of the cost of bearing the selfish cytotype (t), the selfish cytotype can more easily spread if there is leakage than when there is not. As the spread of the selfish cytotype is necessary for the spread of the type-(2+3) the leakage can, at certain parameter values, aid the transition from three to two mating-types.

By simulation it is found that when leakage is slightly greater than transmission (i.e. $(1-\alpha) > k$) the evolution of two sexes is still possible. In large part this is because, although the type-(2+3) cannot always remain in linkage disequilibrium with the selfish cytotype, it can sometimes remain in disequilibrium long enough for the type-2 and type-3 to be eliminated, at which point only two-mating types persist along with the selfish cytotype at fixation. The novel mating-type maintains linkage disequilibrium longer because of its refusal to mate with two of the three other mating-types. Put another way, at relatively low values of cost to not mating (U) it is better not to mate and not contract a disease than to mate. Under other circumstances, the novel type can invade but the selfish cytotype can reach fixation before the elimination of types 2 and 3. Three mating-types and the selfish cytotype will then typically persist, with the novel type being eliminated.

4. MORE THAN THREE MATING-TYPES

Consider now a population with four mating-types. Into this population we can ask about a rare new mating-type that has the alleles of types 3 and 4, again in tight linkage, i.e. a type-(3+4). In general, one might imagine that the conditions for invasion of a type-(3+4) allele into a population with four mating-types would be broader than those for the type-(2+3) into the population with three. This is because, at the point of invasion, only one third of the population are potential mates for the latter, whereas one half are for the former. The type-(3+4) therefore suffers less cost than does the type-(2+3). More precisely, ignoring the effect of the selfish element, at the point of invasion the relative fitness of a type-(3+4) allele coming into a population with four mating-types is:

$$\frac{0.5(1-U) + 0.5}{0.25(1-U) + 0.75}$$

whereas that for a type-(2+3) allele coming into a population with three mating-types is:

$$\frac{0.67(1-U) + 0.33}{0.33(1-U) + 0.67}$$

So long as $U > 0$, the type-(3+4) allele always has a higher relative fitness than the type-(2+3) and the difference in relative fitness increases as the cost to mate finding goes up. We should therefore expect, all other things being equal, that the invasion of a type-(3+4) to be easier than a type-(2+3).

This conclusion, while generally sound, is not always

true, however, as extensions of the model incorporating the effect of the selfish element are sensitive to assumptions about the form of the curve relating the degree of transmission of the selfish cytotype (α and k) to the relative position in the hierarchy, a curve about which we know nothing. As it is of dubious value to go through every possible model in detail, it is perhaps better simply to state that, under a wide variety of models, the supposition that invasion of type-(3+4) is easier than invasion of type-(2+3), is correct and that for most models there exists some small domain in parameter space at which U is too high to allow collapse from three to two, but not so high to allow evolution from four to three.

In general, the relative fitness of a new allele at the mating-type locus that prohibits mating with two other mating-types (e.g. the type-(3+4) or type-(2+3)) is, in the absence of the selfish element, given by:

$$RF_N = \frac{\frac{2}{N}(1-U) + \frac{N-2}{N}}{\frac{1}{N}(1-U) + \frac{N-1}{N}}$$

where N is the number of mating-types. We may then ask how the relative fitness of such a new allele compares with that in a population with one more mating-type, i.e. what is the form of RF_{N+1}/RF_N . For $U > 0$, as N tends to infinity so the ratio of the relative fitness tends asymptotically towards unity. It follows that for high N , if such a mutant mating-type allele can invade, for the reasons outlined above, then at $N-1$ invasion of a comparable allele is also likely. The slope of the ratio in relative fitness greatly increases, however, as N tends towards two. Therefore it is reasonable to suppose that if species are not able to evolve to two mating-types, then the stable number of mating-types is likely to be a relatively low number.

5. DISCUSSION

It is shown that if, into a population with three mating-types, comes a novel mating-type that enables a gamete to mate with only one third of the population, but that can remain in adequately strong linkage disequilibrium long enough with a relatively fit cytotype (i.e. without the putative selfish element) then, despite suffering excessive costs of mate finding, such a mutant can invade. As a consequence, a population can evolve to one having two sexes when initially it had three. In addition, we may predict: (i) that unless costs to mate finding are high, organisms with gametic fusion should evolve towards two mating-types/sexes; (ii) that organisms with gametic fusion and more than two sexes should be rare; (iii) that they should have an ecology consistent with especially costly mate-finding; and (iv) will probably not have a high number of mating-types.

As regards rarity, it has been previously established (Hurst & Hamilton 1992; Hurst 1995) that more than two sexes associated with fusion is an unusual condition

and reported regularly only in slime moulds. Cellular slime moulds have two, three or four mating-types, whereas acellular ones, such as *Physarum polycephalum*, may have as many as 13 alleles at one locus coordinating uniparental inheritance (for references see Hurst 1995). It is however unclear, at least in the case of *Physarum*, how many of the 13 exist in any sub-population. These gametes, being terrestrial and ameoboid, probably face considerable difficulties finding mates.

If costs of mate finding are excessively high (i.e. the new allele can never invade) it is to be expected that cytoplasmic selfish agents may be controlled through preventing the fusion of gametes (Hurst 1990; Hurst & Hamilton 1992). In both ciliates and hymenomycetes, nuclei are exchanged between partners but cytoplasm is not. Both of these groups are, as expected, unusual in often having high numbers of mating-types (Hurst & Hamilton 1992). The number of mating-types in these groups (up to 100 in ciliates, several thousands in hymenomycetes), can be contrasted with the low numbers in slime moulds.

The findings in this paper can be compared with those from the analysis of Iwasa & Sasaki (1987). These authors have shown that if, and only if, the mating kinetic is such that there is effectively no cost to mate finding, then drift should return the system with multiple sexes to one with only two. Under all other circumstances the number of sexes tends towards infinity. There exists no domain within which a low number (greater than two) may persist and no domain within which costly mate finding is consistent with two sexes. This model also does not account for the apparent correlation between high number of mating-types and restrictions on cytoplasmic continuity.

Within a few genera of ciliates species with only two mating-types are found (this is, for example, often reported in species of the genus *Paramecium*). Likewise, in some ascomycete fungi, whereas cytoplasmic organelles are inherited from the female parent, in addition, there exist incompatibility alleles that in some species are binary. These two facts would suggest that forces other than the coordination of cytoplasmic genetics may also play a role in the evolution of some binary mating-types. It is most probably the case that if the cost of mate finding is especially low that stochastic effects (not directly modelled here) will allow some members of a taxa to have only two mating-types.

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