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Selfish DNA and breeding system in flowering plants

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In many species, some individuals carry one or more B chromosomes: extra, or supernumerary chromosomes not part of the normal complement. In most well-studied cases, B's lower the fitness of their carrier and persist in populations only because of accumulation mechanisms analogous to meiotic drive. It has been suggested that such genomic parasites are expected to persist only in outcrossed sexual species, in which uninfected lines of descent can be continuously reinfected; in inbred or asexual species, all selection is between lines of descent, and the genomic parasites are either lost or must evolve into commensals or mutualists. Here we present a simple population genetic model of the effect of outcrossing rate on the frequency of B chromosomes, and find that outcrossing facilitates the spread of parasitic B's, but inhibits the spread of mutualists. Data compiled from the literature on breeding system and B chromosomes of British plants indicate that B's are much more likely to be reported from obligately outcrossed species than inbred species. These results support the ideas that most B chromosomes are parasitic, and that breeding systems play a central role in the biology of selfish genes.

Keywords: B chromosomes, breeding system, mating system, selfish DNA

1. INTRODUCTION

B chromosomes are extra, or supernumerary chromosomes found in some members of a population, but not others (Jones & Rees 1982). In most well-studied cases, B's lower the fitness of their host and persist in populations only because of a superMendelian rate of inheritance, in which they are inherited by more than 50% of the gametes (Östergren 1945; Nur 1977; Jones 1991). This increased rate of transmission usually results from the B preferentially moving during some cell-division towards the germline and away from the soma. This 'gonotaxis' has been observed during meiosis, when not all meiotic products are viable (e.g. female meiosis in plants and animals, male meiosis in some scale insects), and in post-meiotic divisions of pollen grains, especially in grasses. It may also occur premeiotically (avoidance of diploid somatic tissues like roots and leaves), though in no case has it been possible to rule out random non-disjunction of B's with subsequent over-proliferation of the B-containing cells in the germline and, independently, loss of B's in the soma (Jones & Rees 1982; Jones 1991).

B chromosomes are thought to occur in 10–15% of plant and animal species (Jones 1985), but little is known about why they are found in some species and not others. It has long been suggested that outcrossed species are more likely to have B's than inbred species (Moss 1969; Jones & Rees 1982), but, to our knowledge, no comparative analysis has yet been published in support of this claim. More recently, such an association has been suggested to follow from the B chromosome way of life: in inbred or asexual species, all natural selection is between lines of descent, and those without B's will be selected for and go to fixation, whereas in outcrossed species, uninfected lines of descent can be continuously reinfected, and B's can persist by virtue of their biased inheritance (Puertas *et al.* 1987; Bell & Burt 1990; Shaw & Hewitt 1990). Put another way, inbreeding increases the variance of B number among individuals and therefore the efficacy of natural selection in reducing their number. Individuals with multiple B's may also have lower levels of drive than those with only one (Kimura & Kayano 1961; Nur 1977; Thomson 1984), and so average rates of transmission may also be lower in inbred populations.

Breeding system might, therefore, play a fundamental role in the ecology and evolution of B chromosomes, and perhaps other nonMendelian 'selfish' genetic elements (Werren *et al.* 1988). In this paper we demonstrate the logic of this hypothesis with a formal genetic model, and present comparative data on the distribution of B chromosomes in inbred and outcrossed species of plants.

2. MODEL

The transmission genetics of B chromosomes is very diverse, and rather than construct a model general enough to cover all described cases (which would be exceedingly complex), we shall focus on a particular class of B's, those that show nonMendelian inheritance only in female meiosis and only when present as a univalent. In *Lilium callosum*, for example, individuals with 1 B transmit it with probability (0.5) to pollen and probability $d=0.8$ to ovules, whereas in 2 B individuals the B's pair at meiosis and show Mendelian inheritance, all gametes carrying 1

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B (Kimura & Kayano 1961). Taxonomically, female-limited meiotic drive is the most widespread B chromosome accumulation mechanism, having been described in flowering plants, grasshoppers, and mammals (Nur 1977; Jones & Rees 1982; Thomson 1984). Such a system can be modelled by using the formalism of a single locus with two alleles, A (B absent) and B (B present), and three genotypes (0, 1, or 2 B's), as follows.

Consider a model population with non-overlapping generations in which progeny are from either selfed or random matings. Let the frequencies of A and B be p and q, and the frequency of zygotes with 0, 1, and 2 B's be x, y, and z, respectively, where

$$x = p^2 + Fpq,\ \ y = 2pq(1-F),\ \ z = q^2 + Fpq,$$

and F is the inbreeding coefficient, a measure of deviation from Hardy–Weinberg proportions (Falconer 1981). F is usually between 0 and 1, but may be negative (heterozygote excess) in this model due to the sex-limited drive. If these three genotypes have relative survival probabilities of 1, w_1 and w_2, then the frequency of adults with 0, 1, and 2 B's will be

$$x_a = x\frac{1}{\overline{w}},\ \ y_a = y\frac{w_1}{\overline{w}},\ \ z_a = z\frac{w_2}{\overline{w}},$$

respectively, where $\overline{w} = x + yw_1 + zw_2$. Gametes will have either 0 or 1 B, and the frequency of B-containing pollen and ovules will be

$$u = y_a\left(\frac{1}{2}\right) + z_a,\ \ v = y_a d + z_a$$

respectively. Then, the frequency of zygotes with 0, 1, and 2 B's in the next generation will be

$$x' = s\left[x_a + \frac{y_a(1-d)}{2}\right] + t(1-u)(1-v),$$
$$y' = s\frac{y_a}{2} + t[(1-u)v + u(1-v)],$$
$$z' = s\left(\frac{y_a d}{2} + z_a\right) + tuv,$$

where s is the fraction of zygotes derived from selfed matings, and $t = 1-s$ is the fraction from random outcrossed matings. Finally, the frequency of the A and B alleles in this next generation will be

$$p' = x' + y'/2 = \frac{(1-u)+(1-v)}{2},\qquad q' = z' + y'/2 = \frac{u+v}{2},$$

and the new inbreeding coefficient will be $F' = 1 - y'/(2p'q')$.

With these transition equations for one complete generation we can now calculate the fitness of the B allele relative to that of the A as $w_B = (q'/p')/(q/p)$, or

$$w_B = \frac{(1+2d)(1-F)pw_1 + 2(Fp+q)w_2}{2(p+Fq) + (3-2d)(1-F)qw_1}. \qquad (1)$$

(Mathematica v. 2.2.2.1 computer file available from the authors.) The conditions for a B chromosome to invade a population when rare and to fix when common are thus:

$$\lim_{q\to 0}\ w_B = \left(d+\frac{1}{2}\right)w_1 - \left[\left(d+\frac{1}{2}\right)w_1 - w_2\right]F > 1, \qquad (2)$$

and

$$\lim_{q\to 1}\ w_B = \frac{2w_2}{(3-2d)w_1 + [2-(3-2d)w_1]F} > 1. \qquad (3)$$

Depending upon whether these conditions are satisfied, the stable equilibrium frequency may be at 0 (B lost), 1 (B fixed), both 0 and 1 (lost or fixed, depending on initial frequency, with an unstable intermediate equilibrium), or somewhere between 0 and 1 (B status polymorphic) (figure 1). If it exists, the intermediate equilibrium frequency can be found by setting $w_B = 1$ (or $q' = q$) and solving for q:

$$\hat{q} = \frac{(1+2d)(1-F)w_1 - 2(1-Fw_2)}{2(1-F)(2w_1 - w_2 - 1)}. \qquad (4)$$

In this model B chromosomes can show either drive ($d > 0.5$) or drag ($d < 0.5$), and their effects on the host can be either beneficial ($1 < w_1 < w_2$) or deleterious ($w_2 < w_1 < 1$; other possibilities where w_1 is not between 1 and w_2 will not be considered here). Of the four possible combinations of these characters, two do not lead to a stable polymorphism, nor an interaction with breeding system: if a B shows drag and is deleterious, then it will be lost from the population regardless of the breeding system, and if a B shows drive and is beneficial, then it will go to 'fixation', with every individual having 2 B's, again regardless of the breeding system. Note they would then be indistinguishable from the normal A chromosomes by routine cytogenetic surveys. The other two types of B's are those that show drive but are deleterious, and those that show drag but are beneficial, which we will refer to as parasitic and mutualistic B's, respectively. By these definitions, most of the well-studied B's are parasitic (Östergren 1945; Nur 1977; Jones 1991), but some mutualistic B's are known as well (Holmes & Bougourd 1989). We first consider the case of a parasitic B.

As the parameters defining the breeding system in this model (s and t) have no effect on the fate of a B chromosome independent of their effect on the inbreeding coefficient F (i.e. they do not appear in expressions (1)–(4)), it is simpler mathematically to study the effect of changes in the breeding system by first looking at the effect of changes in F. The derivative of w_B with respect to F is

$$\frac{dw_B}{dF} = \frac{-4\{(d-\frac{1}{2})pw_1 + p(w_1 - w_2) + [1-(\frac{3}{2}-d)w_1]qw_2\}}{[(3-2d)(1-F)qw_1 + 2(p+Fq)]^2},$$

and by inspection, this is negative whenever $0.5 < d \leqslant 1$ and $0 \leqslant w_2 < w_1 < 1$, i.e. whenever the B shows drive and is deleterious. Thus, as the inbreeding coefficient F increases, the relative fitness of parasitic B's decreases. Note also that for parasitic B's, conditions (2) and (3) become increasingly difficult to satisfy with increasing F.

Finally, the derivative of the equilibrium frequency with respect to F is

$$\frac{d\hat{q}}{dF} = \frac{1-w_2}{(1-F)^2(1-2w_1+w_2)}.$$

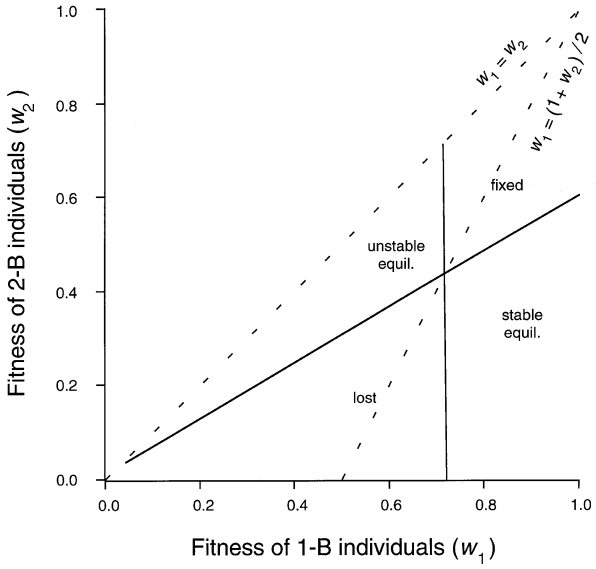

Figure 1. Fate of a B chromosome as a function of its effects on fitness, exemplified here for a parasitic B with $d=0.9$, $F=0.01$, and $w_2 < w_1 < 1$. The solid boundaries are derived from conditions (2) and (3) and intersect along the line defined by $w_1=(1+w_2)/2$ (heterozygote fitness the arithmetic mean of homozygote fitnesses).

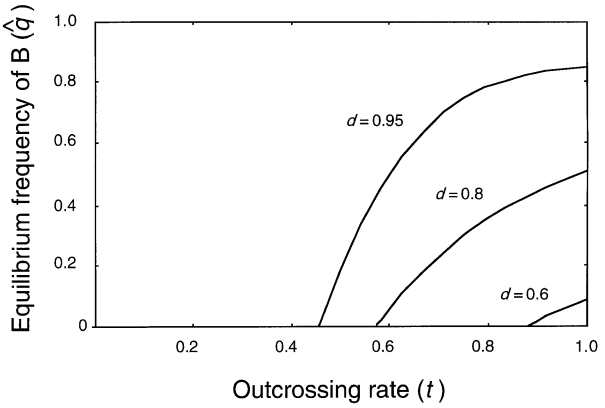

Figure 2. The equilibrium frequency of B-containing individuals as a function of outcrossing rate for parasitic B chromosomes with parameter values appropriate to *Lilium callosum* ($w_1=0.95$; $w_2=0.4$).

If there is an intermediate equilibrium frequency and the heterozygote fitness is greater than the arithmetic mean of the homozygotes, then the equilibrium is stable (see figure 1) and $\hat{q}$ decreases with increasing F; if heterozygote fitness is less than the mean of the homozygotes, then the equilibrium is unstable and $\hat{q}$ increases with increasing F, expanding the zone of attraction for the B to be lost. Either way, an increased F is disadvantageous to the B.

To calculate the effect of the outcrossing rate (t) on the population dynamics of B's directly, we can solve the two equations $w_B=1$ and $F'=F$ simultaneously to get equilibrium values of q and F. These values are too complex for easy analysis (see Appendix), but can be used to examine particular parameter values. As an example, figure 2 shows the equilibrium frequency of parasitic B's with values appropriate to *Lilium callosum* ($d=0.8$, $w_1=0.95$, $w_2=0.4$) (Kimura & Kayano 1961). In obligately outcrossed populations the expected frequency of B's is 0.51, but if the level of outcrossing were to fall, so would the frequency of B's, until they cannot persist for outcrossing rates less than 0.57. Equilibrium frequencies of B-containing individuals are also shown for $d=0.95$ and $d=0.6$.

Changes in breeding system have exactly the opposite effect on mutualistic B's as they do on parasitic B's: increased inbreeding increases the relative fitness of the B, makes it easier to invade and go to fixation, increases the equilibrium frequency when stable, and decreases it when unstable. This is most easily seen by noting that the A allele in our model has the properties of a mutualistic B: beneficial to the organism, but showing meiotic drag. Whatever affects the frequency of the B allele will have an equal and opposite effect on the frequency of A.

3. DATA

We collated data on the mating system of British plants, using the *Biological flora of the British Isles*, published in the *Journal of Ecology* (volumes 42–79, 1952–1991) and the compilation of Grime *et al.* (1988). To our knowledge, the British flora is better characterized for breeding systems than any other. Species were categorized as: (i) predominantly inbreeding; (ii) mixed or mostly outcrossing, but self-compatible; and (iii) partly or completely self-incompatible, or dioecious. Species reproducing vegetatively or apomictically were excluded because they were rare and because without meiosis, it can be difficult to distinguish B's from fragmented A's. Information on B chromosomes was obtained from the *Atlas of B chromosomes* (Jones & Rees 1982), a list of all species reported to have B's.

Data on breeding systems were obtained for 353 species of British plants, of which 44 (12.5%) are reported to have B chromosomes (complete data set available from the authors). To test for an association between breeding system and presence of B's, we did three analyses. First, across all species, B's are reported from 5.5% of selfers, 6.8% of those with mixed mating systems, and 29% of obligately outcrossed species, a very highly significant difference (table 1*a*). Second, the data set is large enough to divide it along taxonomic lines into three groups (Compositae, Gramineae, and everything else) and analyse each separately, and in each group the obligately outcrossed species are significantly more likely to have B's than the others (table 1*b*). Finally, we used the method of independent contrasts (Felsenstein 1988; Burt 1989). A total of 11 genera have variation in both breeding system and presence/absence of B's; after these taxa are removed from the data set, there are six tribes with variation in both characters; and after these are removed, there are two families with variation in both characters, for a total of 19 taxonomically independent contrasts (Burt 1989). The correlation between outcrossing and presence of B's is positive in 16 of these. To assign a p-value, for each contrast we calculated p_+, the probability of observing a positive correlation under the null hypothesis of independence. The latter is calculated by considering all possible permutations of the data with fixed marginals, in the manner of

Table 1. *Breeding system and B chromosomes in British plants*

(Numbers of species with the indicated breeding system and B chromosome status. G. statistics for (*b*) calculated after combining inbred and mixed-mating species.)

	breeding system			G
	inbred	mixed	outcrossed	
(*a*) all data				
B's present	3	14	27	
absent	52	191	66	27.9[c]
(*b*) by taxonomic groups				
		Compositae		
B's present	0	3	7	
absent	3	18	9	4.97[a]
		Graminae		
B's present	2	5	12	
absent	3	23	9	7.26[b]
		the rest		
B's present	1	6	8	
absent	46	150	48	7.75[b]

[a] $p < 0.05$.
[b] $p < 0.01$.
[c] $p < 0.001$.

Fisher's exact test. For example, in a contrast of three species in which two are outcrossed and two have B chromosomes, the probability of observing a positive correlation by chance is 0.3̇3̇ (Sokal & Rohlf 1981). The total expected number of positive correlations is the sum of the p_+'s across contrasts, which in this case is $\Sigma p_+ = 9.8$, with standard error $\sqrt{\Sigma(p_+(1-p_+))} = 2.105$, and the probability of observing 16 or more positive correlations by chance is $p \approx 0.0017$ (one-tailed, from the table of normal deviates).

4. DISCUSSION

Our model confirms previous verbal arguments that parasitic B's are better able to persist in outcrossed species than in inbred ones, and shows the reverse is true for mutualistic B's. The effect of inbreeding is twofold in our model: first, it reduces the frequency of heterozygotes, and so the average level of drive of a B chromosome (which shows accumulation in heterozygotes but not homozygotes). Second, it increases the variance in the number of B's among individuals, and so the efficacy of natural selection in reducing their number. We have also investigated models where the number of B's is not limited to two and B's have a constant probability of transmission regardless of the number of B's. In such a model only the second factor operates, and these show qualitatively similar results: inbreeding is harmful to parasitic B's, but beneficial to mutualistic ones (not shown).

In light of these results, and as most well-studied B's are parasitic rather than mutualistic (Östergren 1945; Nur 1977; Jones 1991), we expected B's to be more common in outcrossed species than inbred ones, and our comparative analysis suggests this is true. This result reinforces the idea that most B's are selfish, for if most were mutualists one would have expected the opposite correlation. Nonetheless,

Table 2. *Independent constrasts analysis*

(Contingency table analysis for 19 independent taxa. For each taxon we show the number of species with the specified breeding system (i-inbred; m-mixed; o-outcrossed) and B chromosome status (top line-present; bottom line-absent), the sign of the correlations between the two, and p_+, the probability of observing a positive correlation under the null hypothesis of independence.)

taxon	i	m	o	sign	p_+
Cirsium	0	1	0		
	0	2	1	−	1/4
Trifolium	0	0	1		
	1	0	2	+	3/4
Papaver[a]	0	0	1		
	2	2	0	+	1/3
Plantago	0	0	1		
	0	1	1	+	2/3
Rumex	0	0	1		
	0	2	1	+	1/2
Ranunculus	0	2	1		
	0	2	3	−	1/2
Alopecurus	0	0	1		
	0	2	0	+	1/3
Avenula	0	0	1		
	0	1	0	+	1/2
Bromus[a]	0	0	1		
	1	2	0	+	1/2
Festuca	0	1	2		
	0	1	0	+	1/2
Luzula	1	0	0		
	0	1	0	−	1/2
Asteraceae	0	0	1		
	0	1	1	+	2/3
Anthemidae	0	2	2		
	0	3	2	+	9/14
Cynarae	0	0	1		
(−*Cirsium*)	0	2	1	+	1/2
Cichorieae[a]	0	0	3		
	1	3	2	+	1/2
Aveneae	0	2	3		
(−*Alopecurus*)	0	8	5	+	13/34
Poeae[a]	1	1	4		
(−*Festuca*)	1	0	2	+	9/14
Campanulaceae	0	0	2		
	0	1	1	+	1/2
Ranunculaceae	0	0	1		
(−*Ranunculus*)	0	1	1	+	2/3

[a] Sign and p_+ calculated from inbred and outcrossed species only.

there are exceptions to the rule, most notably the three species reported to be predominantly inbred and have B's: *Desmazaria* (=*Catapodium*) *rigidum*, *Poa annua* (both Graminae), and *Luzula campestris* (Juncaceae). These reports are of obvious interest, as candidate beneficial B's.

Several limitations of our model and data set must be noted. First, the model considers only a single locus, and selection at other loci, which would tend to interfere with that acting on B's, is ignored. Such interference will be stronger in inbred populations than outcrossed ones, and so will counteract to some extent the effect modelled here (Charlesworth *et al.* 1993). However, selection at other loci seems likely to be of secondary importance, as B's

themselves have relatively large effects on fitness and assort independently of other chromosomes. Second, the data set, though apparently the best currently available, still suffers from some obvious shortcomings. The data on breeding systems and B chromosome status are not from the same population, and both are known to vary among populations within species. Also, variance in study effort must presumably account for some of the variance in B chromosome status, though how much is not clear (and note that all species considered have been studied to the extent that information on haploid chromosome numbers are available). Finally, we have made no attempt in our model or analysis to allow for species' differences either in the rate at which B chromosomes arise or in their long-term evolutionary stability, as so little is known of these factors. Nevertheless, not all outcrossed species have B chromosomes, and something else remains to be accounted for.

Breeding system is likely to be important in determining the distribution of other selfish genes too (Hickey 1982; Futcher *et al.* 1988), though comparative data are so far lacking. Indeed, the model presented here can be applied without change to meiotic drive genes, and for those that are sufficiently deleterious when homozygous that they cannot go to fixation (e.g. *t* in *Mus* and *SD* in *Drosophila*, Lyttle 1991), their equilibrium frequency is expected to decline as outcrossing declines, until at some point they are lost from the population (Petras 1967). On the other hand, meiotic drive genes that are homozygous normal and thus expected to go to fixation (e.g. spore-killers in various ascomycete fungi, Turner & Perkins 1991) will do so more slowly in inbred species than outcrossed ones, and so are more likely to be detected (assuming mutations are not limiting). Perhaps it is for this reason that at least five different spore-killing systems have been found in the pseudohomothallic (and thus presumably very highly inbred) *Podospora anserina* (M. van der Gaag and R. Hoekstra, personal communication). Outbred populations will also be more susceptible to invasion by transposable elements (Hickey 1982; Zeyl *et al.* 1994, 1996), though natural selection may also be more efficient in removing them from the population (Charlesworth & Charlesworth 1995), and the overall effect on frequencies is difficult to predict. Finally, cytoplasmic male sterility genes are expected to be more common in partly inbred species than in obligately outcrossed ones because avoidance of inbreeding is probably a large part of their advantage (Kaul 1988). Breeding system is a key parameter in the biology of selfish genes.

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APPENDIX 1

For given values of w_1, w_2, d, and t, the equilibrium inbreeding coefficient is:

$$\hat{F} = \frac{k_1^2 - k_1 k_3 k_4 - k_4^2 k_5}{3 k_1 k_4^2},$$

where

$$k_1 = \sqrt[3]{\frac{-k^2 k_4^3 + \sqrt{k_4^6\left(k_2^2 + 4k_5^3\right)}}{2}};$$

$$k_2 = -k_3^3 - 3k_3 k_5 + 27\, k_4 k_6;$$

$$k_3 = 4dsw_1 - (5 + 12de)w_1^2 + 4(1 + t)w_2 + 4esw_1 w_2;$$

$$k_4 = [2 - (3 - 2d)w_1][-(1 + 2d)w_1 + 2w_2];$$

$$k_5 = 4\begin{bmatrix} (-3 - 6ds - 4d^2 s^2 + 12det)w_1^2 \\ +2(3 + 2ds - 12det)w_1^3 - 4w_1^4 \\ +4(3 + 4d - 2dt)sw_1 w_2 + 2(-10 - 4des^2 \\ \qquad +11t + 12det)w_1^2 w_2 \\ +2(3 + 2es - 12det)w_1^3 w_2 - 4(4s + t^2)w_2^2 \\ +4(3 + 4e - 2et)sw_1 w_2^2 + (-9 + 6d - 4e^2 s^2 \\ \qquad +6et + 12det)w_1^2 w_2^2 \end{bmatrix};$$

$$\begin{aligned} k_6 = {} & -2(3 - 2d)(1 + 2ds - 4det)w_1^3 \\ & +(2d - 1)^2(3 + 4de)w_1^4 \\ & -16sw_2^2 + 8sw_1 w_2(1 + w_2) \\ & +4(2 + 8de - t - 12det)w_1^2 w_2 \\ & -2(3 + 4de - 8dt + 8d^3 t - 2et)w_1^3 w_2; \end{aligned}$$

$e = 1 - d$; and

$s = 1 - t$.

The equilibrium frequency of the B chromosome can be found by substituting this into equation (4) of the text.

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