Sex ratio evolution in lemmings

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In the varying lemming, *Dicrostonyx torquatus*, numerous XY females occur due to the X-linked mutation X*. Gileva (1987) has shown that there is also segregation distortion in males, with the segregation ratio for Y sperm being about 0·56, which has a significant effect on the sex ratio and the frequency of XY females. A theoretical analysis shows that this degree of segregation distortion is expected to evolve in the *Dicrostonyx* system under random mating, provided that reproductive compensation for the loss of YY zygotes by XY females is largely an automatic process due to reduced competition between the surviving embryos. The evolution of segregation distortion makes it unlikely that X* is an adaptation to allow a female-biased sex ratio in response to population structure.

INTRODUCTION

The wood lemming, *Myopus schisticolor*, and the varying lemming, *Dicrostonyx torquatus*, have two types of X chromosome, X^0 which behaves normally and X* which suppresses the male-determining property of the Y chromosome (reviewed by Bull and Bulmer, 1981). All males are X^0Y, while there are three female genotypes, X^0X^0, $X*X^0$ and X*Y. X*Y *Myopus* females produce only X* ova and so have all-female litters. X*Y *Dicrostonyx* females segregate both X* and Y ova and so produce some inviable YY zygotes, but there is at least partial reproductive compensation for this loss of fertility (Gileva *et al.*, 1982; Gileva, 1987).

The X* chromosome is maintained in the population by segregation distortion in X*Y *Myopus* females and by reproductive compensation in X*Y *Dicrostonyx* females. However, Bull and Bulmer (1981) pointed out that the observed proportion of males is lower in both species and the frequency of X*Y females is higher than predicted on the assumption that segregation and fertility are otherwise normal. Gileva (1987) has recently shown that there is segregation distortion in favour of Y sperm in *Dicrosonyx* males, which explains the discrepancy in that species. (A paradoxical feature of the system is that segregation distortion in favour of Y sperm decreases the population sex ratio at equilibrium.) Bull and Bulmer (1981) previously showed that segregation distortion in favour of Y sperm might be expected to evolve on theoretical grounds in the *Myopus* system. I here extend that analysis to the *Dicrostonyx* system.

METHODS AND RESULTS

Suppose that segregation of the sex chromosomes in males is controlled by an autosomal locus with two alleles, A and a, such that aa males produce r Y and $(1-r)$ X^0 sperm while Aa males produce s Y and $(1-s)$ X^0 sperm; the mutant A allele is assumed to be rare so that the AA genotype can be ignored under random mating. I shall determine the conditions under which A will increase in frequency when it is rare, and hence find the evolutionarily stable segregation ratio which cannot be invaded by any rare mutant.

To model the *Dicrostonyx* system, I suppose that there is no segregation distortion in females, but that there is some reproductive compensation for the loss of YY zygotes in X*Y females. Suppose that X^0X^0 and $X*X^0$ females on average have n surviving offspring. A fraction $\frac{1}{2}r$ of the zygotes of X*Y females mated to aa males are YY, and I suppose that these females have $(1-\frac{1}{2}r(1-c))n$ surviving non-YY offspring, where c represents the degree of reproductive compensation for the loss

of YY zygotes, ranging from 0 (no compensation) to 1 (full compensation). I consider two models of compensation in matings of X*Y females to Aa males. If compensation is an *automatic* property of the reproductive system, due for example to decreased competition between the remaining embryos as a result of the early loss of YY zygotes, then these mothers will have $(1 - \frac{1}{2}s(1 - c))n$ surviving non-YY offspring. If compensation is an *evolved* property, due for example to an increased ovulation rate in X*Y females, they will have $(1 - \frac{1}{2}s)(1 - \frac{1}{2}r)^{-1}(1 - \frac{1}{2}r(1 - c)n$ surviving non-YY offspring when mated to Aa males.

In the absence of A, the relative frequencies at equilibrium (summing to 1) of the three female genotypes X^0X^0, X^*X^0 and X^*Y under this model are

$$y_1 = 1 - y_3/r$$
$$y_2 = (1 - r)y_3/r \tag{1}$$
$$y_3 = (r^2(c - 2) + 5r - 2)/(r(c - r + 2))$$

and the sex ratio (proportion of males) is

$$(r(1 - y_3) + (1 - r)y_3 rc/(4 - 2r))/(1 - \tfrac{1}{2}ry_3(1 - c)). \tag{2}$$

(See Bull and Bulmer, 1981, table 2.) Let $x = (x_1, x_2, x_3, x_4)$ be the column vector of the relative frequencies of the genotype Aa in X^0X^0, X^*X^0, X^*Y and X^0Y individuals respectively, all supposed to be small. The linearised recurrence relationship for x under random mating is $x' = Ax$, with

$$a_{11} = \tfrac{1}{2}y_1/(y_1 + \tfrac{1}{2}y_2)$$
$$a_{12} = \tfrac{1}{2} - a_{11}$$
$$a_{13} = 0$$
$$a_{14} = \tfrac{1}{2}(1 - s)/(1 - r)$$
$$a_{21} = a_{31} = 0$$
$$a_{22} = a_{32} = \tfrac{1}{2}y_2/(y_2 + y_3 f)$$
$$a_{23} = a_{33} = \tfrac{1}{2} - a_{22}$$
$$a_{24} = \tfrac{1}{2}(1 - s)(y_2 + y_3 f^*)/((1 - r)(y_2 + y_3 f)) \tag{3}$$
$$a_{34} = \tfrac{1}{2}s(y_2 + y_3 f^*)/(r(y_2 + y_3 f))$$
$$a_{41} = \tfrac{1}{2}ry_1/d$$
$$a_{42} = \tfrac{1}{4}ry_2/d$$
$$a_{43} = \tfrac{1}{4}(1 - r)y_3 f/d$$
$$a_{44} = (\tfrac{1}{2}s(y_1 + \tfrac{1}{2}y_2) + \tfrac{1}{4}(1 - s)y_3 f^*)/d$$

$$d = r(y_1 + \tfrac{1}{2}y_2) + \tfrac{1}{2}(1 - r)y_3 f$$
$$f = (1 - \tfrac{1}{2}r)^{-1}(1 - \tfrac{1}{2}r(1 - c))$$
$$f^* = \begin{cases} (1 - \tfrac{1}{2}s)^{-1}(1 - \tfrac{1}{2}s(1 - c)) \\ \quad \text{under } automatic \text{ compensation} \\ f \quad \text{under } evolved \text{ compensation.} \end{cases}$$

The rare mutant A coding for the segregation ratio s will increase in frequency if the dominant eigenvalue of A is greater than 1. The condition for r to be the evolutionarily stable segregation ratio is that no rare mutant with $s \neq r$ can invade. This value can be found by solving the equation

$$\frac{\delta}{\delta s} \det (A - I)\big|_{s = r} = 0, \tag{4}$$

(Taylor and Bulmer, 1980). This equation was solved numerically for different degrees of reproductive compensation. The results are shown in table 1, together with the resulting sex ratio and the proportion of XY females from equations (1) and (2); the latter quantities are also shown for comparison when there is no segregation distortion $(r = \tfrac{1}{2})$. It will be seen that greater segregation distortion is expected to evolve under automatic than under evolved compensation. The reason is that when $s > r$, the degree of reproductive compensation in matings of Aa males with X*Y females is greater under automatic than under evolved compensation, making it easier for the mutant to spread. The selection pressure for segregation distortion for Y in males derives from the female-biased sex ratio, which generates selection to increase the sex ratio under random mating. A paradoxical consequence of the evolution of segregation distortion is that it actually decreases the sex ratio further by facilitating the spread of the X* chromosome.

Data presented by Gileva (1987) show that the estimated segregation ratio for Y in *Dicrostonyx* males is 0.56 ± 0.01, the sex ratio being 0.37 ($n = 3475$) and the frequency of XY among females 0.36 ($n = 1320$). It will be seen from table 1 that the observed sex ratio and frequency of XY females can be accounted for by the observed level of segregation distortion, given that there is about 75 per cent reproductive compensation, and that the observed level of segregation distortion can be explained on evolutionary principles provided that reproductive compensation is primarily an automatic rather than an evolved characteristic. Gileva *et al.* (1982) have shown that there is a higher ovulation rate in XY than in XX females, suggesting that compensation is evolved, but this does not exclude the possibility that it also has a major automatic component. Further study of the nature of compensation in natural populations is needed.

Table 1 Predicted segregation ratio for Y in *Dicrostonyx* males (r) and its effect on the sex ratio (SR) and the relative frequency of XY females (y_3) as a function of the degree of reproductive compensation (c)

c	Evolved compensation			Automatic compensation			No distortion ($r = \frac{1}{2}$)	
	r	SR	y_3	r	SR	y_3	SR	y_3
1·00	0·52	0·41	0·25	0·60	0·37	0·45	0·42	0·20
0·75	0·51	0·43	0·21	0·57	0·40	0·35	0·43	0·17
0·50	0·51	0·44	0·16	0·53	0·43	0·23	0·45	0·12
0·25	0·51	0·47	0·09	0·51	0·47	0·11	0·47	0·07
0·00	0·50	0·50	0·00	0·50	0·50	0·00	0·50	0·00

DISCUSSION

It has been assumed that segregation distortion for Y sperm can occur without loss of fertility. If segregation distortion were inevitably accompanied by some loss of fertility then its evolution would clearly be hampered. It has also been assumed, following Gileva (1987), that there is an autosomal gene acting in males leading to preferential production of Y sperm, but the breeding data are equally consistent with a gene acting in all three types of female leading to preferential fertilisation by Y sperm. Further investigation is needed to clarify the proximate causes of segregation distortion, which is a problem of general interest because of the increasing evidence of adaptive control of sex ratios in mammals.

Bull and Bulmer (1981) showed by a similar argument in *Myopus* (in which X*Y females produce only X* ova) that the optimal segregation ratio for Y in males is 0·64. With this segregation ratio, the population sex ratio should be 0·18 (compared with 0·25 with no bias) and the relative frequency of XY females should be 0·56 (compared with 0·33 with no bias). There is no direct evidence about the level of segregation distortion in *Myopus* males, but in one captive colony the observed sex ratio was 0·25, consistent with unbiased segregation, while in another the sex ratio was 0·19 and the frequency of XY females was 0·48, consistent with segregation distortion at the predicted level. Further investigation is required.

It has been suggested that the existence of the X* karyotype is associated with the population cycles of lemmings which make a female-biased sex ratio adaptive (Maynard Smith and Stenseth, 1978; Bulmer and Taylor, 1980; Bull and Bulmer, 1981). In a random mating population a female-biased sex ratio is non-adaptive so that an autosomal suppressor of X* activity should spread through the population once it has arisen; in a geographically structured population with local

mate competition or interdemic selection favouring a female-biased sex ratio, such an autosomal suppressor would not spread. On this interpretation the X* system is protected from suppression in lemmings by the break-up of the population into a large number of small isolated demes during a population crash, giving rise to selection for a female-biased sex ratio.

The existence of segregation distortion for Y in males casts doubt on this theory for two reasons. Firstly, if this type of segregation distortion is possible without loss of fertility, it provides a much more straightforward way of adjusting the sex ratio to its optimal level. Secondly, the level of segregation distortion observed in *Dicrostonyx* (and inferred in one *Myopus* population) is consistent with the level predicted under random mating; selection for a female-biased sex ratio due to population structure would abolish the selection pressure for segregation distortion for Y sperm. It is therefore suggested that the X* karyotype in lemmings is an historical accident which only exists because an appropriate suppressor has not yet arisen.

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