

Sex Ratio Under the Haystack Model†

M. G. BULMER‡ AND P. D. TAYLOR

*Department of Mathematics and Statistics, Queen's University,
Kingston, Ontario, Canada*

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This paper investigates the evolution of the sex ratio under an extension of the haystack model of Maynard Smith (1964). At the beginning of each season a stack is colonized by a number of fertilized females, and their offspring breed there for several generations until new haystacks are available for colonization. We intend this as a model for populations which undergo periodical population explosions and crashes. With mating before dispersal, the number of generations in the stack has little effect on the equilibrium sex ratio, but it has a marked effect with mating after dispersal. This model is then used to investigate the evolutionary stability of the mechanism of sex determination found in the wood lemming which leads to a population sex ratio of three females to one male.

1. Introduction

It has been known since Hamilton's (1967) paper on local mate competition that inbreeding can lead to the evolution of a biased sex ratio. We have argued elsewhere (Taylor & Bulmer, 1980*a,b*; Bulmer & Taylor, 1980) that the effect of inbreeding on the sex ratio can only be understood in terms of the processes which give rise to inbreeding. In the present paper we shall consider the evolution of the sex ratio under a model based on the haystack model of Maynard Smith (1964), in which a species of mouse lives entirely in haystacks.

At the beginning of each breeding season a stack is colonized by a number of fertilized females, and their offspring breed there for several generations until the following year, when new haystacks are available for colonization. In section 2 we suppose that females mate with males from their own colony before dispersal, and in section 3 that they mate at random with males from other colonies after dispersal. [We feel that this model provides a paradigm for populations such as those of some rodents, which undergo periodical

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‡ Permanent address: Department of Biomathematics, Pusey Street, Oxford.

population explosions followed by crashes, after which the population retreats into small isolated refuges; we envisage the type of ecological situation discussed by Stenseth (1978).] In section 4 we investigate the evolutionary stability of the genetic mechanism of sex ratio determination found in the wood lemming under the ecological model outlined above; this problem has been considered previously by Maynard Smith & Stenseth (1978).

2. The Haystack Model with Mating Before Dispersal

The model to be considered is as follows. The environment consists of a large number of haystacks, each of which is colonized by N fertilized females at the beginning of a breeding season. Each female has offspring and dies, the male and female offspring within a stack mate at random with each other to produce grandchildren, who in turn mate with each other to produce great-grandchildren, and so on. This process continues for G generations until the end of the year, when new haystacks are available for colonization. Fertilized females disperse at random to colonize these stacks and restart the cycle; when each stack has been colonized by N females, any remaining females die without reproducing. Note that the "fitness" of a stack at the end of the season is proportional to the number of females in it. This generates selection pressure for a female-biased sex ratio, whereas there is selection for a sex ratio of $\frac{1}{2}$ during the season, when breeding occurs within the stack, by the usual Fisherian argument. When $G = 1$ this model reduces to Hamilton's (1967) model, which has been discussed in another paper (Taylor & Bulmer, 1980a). In that paper we stressed competition between brothers for mates as an alternative way of explaining the tendency towards a female-biased sex ratio.

To investigate the equilibrium sex ratio under this model we consider a locus with two alleles, R and S , with S dominant to R . We suppose that the gene acts in females, so that RR females produce offspring with sex ratio r , while SR or SS females produce offspring with sex ratio s , whatever the genotypes of their mates. It makes no difference whether the gene is supposed to act in females (as we have done) or in males.

There are nine possible genotypes of a fertilized female, which may be represented by (i, j) , where i denotes the number of S genes in the female and j the number in her mate ($i, j = 0, 1, 2$). A pair will be called non-mutant if both the female and her mate are RR ($i + j = 0$), and mutant otherwise. We suppose that S is rare, so that the possibility that there are two or more mutant pairs in a stack at the beginning of a season can be ignored. Write $x(i, j)$ for the frequency at the beginning of a season of stacks with one

mutant pair of type (i, j) and $N - 1$ non-mutant pairs, which will be called a mutant stack of type (i, j) ; since S is rare the $x(i, j)$'s will be small.

To determine whether S will spread when it is rare we find the linearized recurrence relations for the frequencies of the eight types of mutant stack from one year to the next, and then calculate the dominant latent root, $\lambda(r, s)$, of the corresponding 8×8 matrix. S will increase or die out according as $\lambda(r, s)$ is greater than or less than 1 in absolute value. The equilibrium sex ratio which will resist invasion by any mutant sex ratio is the value of r such that $|\lambda(r, s)| < 1$ for all $s \neq r$.

This equilibrium sex ratio has been found by numerical investigation of the function $\lambda(r, s)$ on a computer, and is tabulated in Table 1 for different

TABLE 1
*The equilibrium sex ratio under the haystack model
with mating before dispersal*

G					
N	1	2	4	8	
1	0	0	0	0	
2	0.250	0.249	0.244	0.242	
4	0.375	0.375	0.373	0.372	
8	0.438	0.437	0.437	0.437	
∞	0.500	0.500	0.500	0.500	

values of N (the number of founding females) and G (the number of generations of breeding within the stack before dispersal). When $G = 1$, the equilibrium sex ratio is

$$r = \frac{1}{2}(N - 1)/N; \quad (1)$$

this is the sex ratio under Hamilton's model in a diploid population. As G increases there is a consistent but very slight decrease in the sex ratio. It can be concluded that, if females mate before dispersal, the number of generations of mating within the stack has a negligible effect on the equilibrium sex ratio. In interpreting this result it must be remembered that the population within the stack is allowed to grow without limit; if population growth were restricted to a finite carrying capacity by density-dependent factors, the sex ratio would tend to $\frac{1}{2}$ as G increases. The increase in the sex ratio with N is due to the increase in the amount of competition between brothers for mates. Alternatively, one can argue that the importance of within-stack competition, favouring a sex ratio of $\frac{1}{2}$, increases with N , while the amount of between-stack competition, favouring a female bias, remains constant.

3. The Haystack Model with Random Mating After Dispersal

We assumed in the last section that females mate within their own stack at the end of the year before dispersing to found new colonies. In this section we make the alternative assumption that unmated males and females disperse at the end of the year, and that individuals from all stacks mate at random with each other before fertilized females (or mated pairs) found new colonies. It would seem that this model is more likely to be appropriate to populations of small rodents which we have in mind.

The equilibrium sex ratio was found in the same way as before, but it was only necessary to consider four types of mutant stack because with population-wide random mating there is a negligible chance that two rare mutant individuals will mate at the beginning of the year. The results are shown in Table 2.

TABLE 2
The equilibrium sex ratio under the haystack model with random mating after dispersal

$G \backslash N$	1	2	4	8	1024
1	0.5	0.312	0.203	0.175	0.149
2	0.5	0.391	0.334	0.312	0.292
4	0.5	0.441	0.412	0.399	0.386
8	0.5	0.470	0.455	0.447	0.440
∞	0.5	0.500	0.500	0.500	0.500

In each column the female bias in the sex ratio decreases with increasing N ; as in Table 1 this results from less competition between brothers for mates. When $G = 1$ there is random mating with no local mate competition so that $r = \frac{1}{2}$. As G increases each row shows an increasing female bias since larger values of G result in a higher proportion of local mate competition to random mating, and hence a more female-biased sex ratio. Note that when $N = 1$, $G = 2$, the sex ratio agrees with the result $r = \frac{5}{16}$ obtained by Maynard Smith (1978, p. 161) by an unspecified argument for a population which mates randomly and brother-sister in alternate generations.

4. Sex Ratio in the Wood Lemming

The wood lemming (*Myopus schisticolor*) has a sex ratio at birth of about three females to one male (Kalela & Oksala, 1966). Fredga *et al.* (1976, 1977) hypothesize that there are two types of X chromosomes, X and X^* .

The X^* chromosome overrides Y , so that X^*Y individuals are female and produce only X^* -carrying ova; X^*X females produce X^* and X ova in equal numbers. Thus there are three types of females (XX , X^*X and X^*Y) but only one type of male (XY).

Bengtsson (1977) has shown that under random mating there is an ecologically stable equilibrium with each of the four genotypes present in equal numbers, so that there are three females to each male, if each of the three mating types is equally fertile. In this section we shall consider whether this genetic system is evolutionarily stable, in the sense of being able to resist invasion by a modifier gene which suppresses the action of X^* , under the breeding structure of section 3. Maynard Smith & Stenseth (1978) have considered the evolutionary stability of this system under inbreeding, but without specifying how inbreeding is produced.

We first consider ecological stability in the absence of modifiers under the breeding structure of the last section in the case $N = 1$. We have postulated discrete, non-overlapping generations, but a problem arises when the founding female is X^*Y , since all her offspring are female and have no brothers to mate with. We suppose in this case that in a proportion p of the cases a male is found to inseminate the daughters (perhaps their father) and with probability $1-p$ no male appears and the colony dies. The problem arises only in the first generation; if a mate is found for the daughters, they should have enough sons to inseminate the next generation of females.

To find the equilibrium frequencies of the four genotypes XX , X^*X , X^*Y and XY we must look at the output, after G generations, of each of the three types of mated females. Assume that, in each generation, a female produces $2k$ offspring. A routine calculation shows that, after G generations, an XX mated female produces $k^G XX$ females and $k^G XY$ males, an X^*X mated female produces $k^G (3/2)^{G-1}/2$ of each of the four genotypes, and, in a proportion p of the cases, an X^*Y female produces $k^G [(3/2)^{G-1} - 1]$ of each of XX and XY and $k^G (3/2)^{G-1}$ of X^*X and X^*Y . It is seen from these outputs that, at equilibrium, XX and XY have the same frequency a and X^*X and X^*Y have the same frequency b . When $G = 1$ and $p < \frac{1}{2}$ or when $G = 2$ and $p < \frac{1}{6}$ these frequencies are $a = \frac{1}{2}$, $b = 0$; in all other cases

$$\begin{aligned} a &= [(1+2p)(\frac{3}{2})^{G-1} - 2p]/D \\ b &= [(1+2p)(\frac{3}{2})^{G-1} - 2]/D, \end{aligned} \tag{2}$$

where D is chosen so that $2a + 2b = 1$. Following the analysis of Bengtsson (1977) we find that these equilibria are globally stable.

We shall now consider evolutionary stability against invasion by modifier genes. We consider two types of modifiers, a Y -linked suppressor, Y^* , such

that X^*Y^* individuals are normal males, and an autosomal suppressor, A^* , such that A^*AX^*Y or $A^*A^*X^*Y$ individuals are normal males, whereas AA^*X^*Y individuals are female. We postulate the breeding structure of the last section with $N=1$ and with the modification defined in the last paragraph. The Y^* problem is simple enough to be handled analytically, but the A^* problem required the use of a computer.

To investigate the Y^* problem, we suppose that Y^* is rare, so that two types of mutant males, XY^* and X^*Y^* , are both rare. We remark that the X^*Y^* male can produce X^*X^* females, but if Y^* is rare, so also will be this type of female, and we can assume that in the random mating phase, such females do not mate with Y^* males. Indeed we can assume that in the random mating phase, each of the two types of Y^* males choose mates XX , X^*X and X^*Y in equilibrium proportions a , b and b . To determine whether Y^* increases or decreases, when rare, we proceed in the usual way. We find the matrix which relates the numbers of successfully mated Y^* males of each type to the numbers of the previous season. Then Y^* invades the population if the dominant eigenvalue of this matrix is greater than unity.

After some straightforward calculations the transition matrix is found to be

$$\mathbf{A} = \frac{1}{M} \begin{pmatrix} a + b[1 + (-2)^{-G}] & b[1 - (-2)^{-G}] \\ (2a + b)[1 - (-2)^{-G}]/3 & [(a + 5b) + (2a + b)(-2)^{-G}]/3 \end{pmatrix} \quad (3)$$

where

$$M = a - pb + \left(\frac{3}{2}\right)^{G-1} \left(p + \frac{1}{2}\right)b. \quad (4)$$

The dominant right eigenvector of \mathbf{A} is $(1, 1)$ with eigenvalue $(a + 2b)/M$. The condition that Y^* will not invade is therefore that $a + 2b < M$, which becomes

$$\left(\frac{3}{2}\right)^{G-1} > (4 + 2p)/(2p + 1). \quad (5)$$

The results are tabulated in Table 3. When $G \leq 2$, Y^* will always invade, and when $G \geq 5$, Y^* will never invade. For $G = 3$ or 4, Y^* will invade if p is sufficiently small.

To investigate stability against invasion by an autosomal modifier, we proceed in the same way. There are now ten genotypes which incorporate at least one A^* , six of which are female and four male. The transition matrix \mathbf{A} is now 10×10 instead of 2×2 , and we used a computer program to calculate its entries and eigenvalues given values of p and G . The condition that the dominant eigenvalue of this matrix be less than one is tabulated in Table 3. It is seen that A^* always invades if $G \leq 3$ and never invades if $G \geq 10$. For

TABLE 3
 Range of values of p for which X^* is
 evolutionarily stable

G	Y^* modifier	A^* modifier
1	none	none
2	none	none
3	$p > 0.70$	none
4	$p > 0.13$	$p > 0.97$
5	all p	
6	all p	$p > 0.52$
8	all p	$p > 0.19$
10	all p	all p

intermediate values of G , A^* will invade if p is sufficiently small. We note that X^* can resist invasion from Y^* more easily than from A^* . We also note that our analysis only considers the conditions under which X^* can resist the spread of modifiers; we have not considered the ultimate fate of the system under conditions when modifiers initially increase.

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