UNISEXUAL SELECTION AT AN AUTOSOMAL LOCUS

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Received April 19, 1968

IN a recent paper (CANNINGS 1967; which will be referred as C) the author considered natural selection at a sex-linked locus with two alleles. It was shown that the existence of a stable non-degenerate equilibrium ensured convergence to that equilibrium. Previous work had established necessary and sufficient conditions for stability (BENNETT 1958; EDWARDS 1961; MANDEL 1959) but no attempt had previously been made to establish convergence.

In this paper we consider a diallelic autosomal locus with selection on the females only. The population is assumed to be large, and mating entirely at random. The methods employed in C will be used to establish sufficient conditions for stability of the unique non-degenerate equilibrium.

For convenience it is assumed that the reader is familiar with the arguments used in C.

The basic equations: Suppose we have alleles A and a, and that the viabilities of AA, Aa and aa are a , h , b respectively for the females, and unity for the males. The gene ratios (frequency of A/frequency of a) will be denoted by f and m for females and males, respectively, and a subscript will denote the generation under consideration. Thus the relative frequencies of the genotypes in the $(N + 1)^{\text{th}}$ generation at birth and at maturity (after selection) are given below, in terms of those in the N^{th} generation.

Stage	Sex	AA	Aa	aa
Birth	Males and females	$f_N m_N$	$(f_N + m_N)$	1
Maturity	Females	$af_N m_N$	$h(f_N + m_N)$	b
Maturity	Males	$f_N m_N$	$(f_N + m_N)$	1

From this we obtain simultaneous recurrence formulae

$$f_{N+1} = \frac{2af_N m_N + h(f_N + m_N)}{2b + h(f_N + m_N)} \quad (2)$$

and

$$m_{N+1} = \frac{2f_N m_N + (f_N + m_N)}{2 + (f_N + m_N)}. \quad (3)$$

Equilibrium: For equilibrium we write $f_N = f_{N+1} = \hat{f}$, $m_N = m_{N+1} = \hat{m}$ and hence

$$\hat{f} = \hat{m} = \frac{h-b}{h-a}, \quad (4)$$

which is the equilibrium found if selection is the same in the males as in the fe-

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FIGURE 1.—Sequences initiated by equal gene-frequencies for males and females (i.e. $f_0 = m_0$), and converging monotonically to the non-degenerate equilibrium (i.e. $h > a, b$).

males (viabilities a, h and b). Since $\hat{f}$ and $\hat{m}$ are gene ratios and hence positive we require (i) $h > b$ and $h > a$

or (ii) $h < b$ and $h < a$.

Convergence and Stability: The condition $h > a$, and hence $h > b$, will be shown to be sufficient for convergence, irrespective of the initial gene frequencies (other than fixation). In addition this condition will be shown to be both necessary and sufficient for stability.

The proof differs from that of C since we must deal with simultaneous sequences $\{f_N\}$ and $\{m_N\}$.

Proofs: (i) In a similar manner to C it can be demonstrated that if $h > a$ and $f_0 = m_0$ then $\{f_N\}$ and $\{m_N\}$ converge to $\hat{f} = \hat{m}$ monotonically (Figure 1).

(ii) The general problem requires an investigation of $\{f_N\}$ and $\{m_N\}$ when $f_0 \neq m_0$. Consider two pairs of sequences of female and male gene-ratios, $\{H_N\}$ and $\{K_N\}$, $\{L_N\}$ and $\{J_N\}$, H and L corresponding to the females, K and J to the males. Let $H_0 = K_0$, $L_0 = J_0$, $H_0 > L_0$ and thence $K_0 > J_0$. Then, by arguments similar to those of C (iii), we have that $H_N > L_N$ and $K_N > J_N$ for all N . Thus if

we have f_0 and m_0 , where $f_0 > m_0$, and we define the above sequences by $H_0 = K_0 = f_0$ and $L_0 = J_0 = m_0$ then for all N , we can show that

$$H_N > f_N > L_N \text{ and } K_N > m_N > J_N.$$

Pairs of sequences such as $\{H_N\}$ and $\{K_N\}$, $\{L_N\}$ and $\{J_N\}$ have been shown to converge to the limit $\hat{f} = \hat{m}$. We now have that $\{f_N\}$ and $\{m_N\}$ are each bounded above and below by sequences converging to $\hat{f} = \hat{m}$, and hence both sequences must converge (Figures 2 and 3).

FIGURE 2

FIGURE 2.—Sequences initiated by unequal gene-frequencies for males and females (i.e. $f_0 \neq m_0$), and converging to the non-degenerate equilibrium (i.e. $h > a, b$). Each sequence being bounded by two monotonic convergent sequences. Initial values f_0 and m_0 on the same side of the non-degenerate equilibrium.

FIGURE 3

FIGURE 3.—As per Figure 2, but initial values f_0 and m_0 on different sides of the non-degenerate equilibrium.

This concludes the proof that $h > a$ is a sufficient condition for convergence. In a similar way to C we can show it is sufficient for stability.

The behavior of the sequences for $h < a$ again parallels the treatment in C.

We can now prove that $h > a$ is a necessary condition for stability. Stability requires that there should exist a spherical neighborhood around the equilibrium, such that the system will return to the equilibrium for any perturbation within that neighborhood. Thus if $h < a$ and a perturbation leads to m and f on the same side of $\hat{m} = \hat{f}$, then the system would move away from the equilibrium. Hence

$h > a$ is a necessary condition for stability; its sufficiency has been proved above.

These results are precisely those which we should obtain for identical selections in the two sexes. Differences in conditions will occur between the two situations when we consider multiallelic systems.

SUMMARY

In this paper the methods of CANNINGS (1967) have been extended to deal with the autosomal diallelic locus with unisexual selection. Sufficient conditions for convergence, and necessary and sufficient conditions for stability, are obtained. These conditions are identical with those for the autosomal locus with equal selection in the two sexes, and constitute an extension of the idea of heterozygote advantage.

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