

EQUILIBRIUM, CONVERGENCE AND STABILITY AT A SEX-LINKED LOCUS UNDER NATURAL SELECTION

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MANY authors (BENNETT 1958; EDWARDS 1961; HALDANE 1923–26; HALDANE and JAYAKAR 1964; KIMURA 1960; MANDEL 1959; SHAW 1959; and SPROTT 1957) have discussed the behaviour of a sex-linked locus under natural selection. The discussion included in these papers has been entirely confined to the investigation of the existence and stability of nondegenerate equilibria. This is an important problem, but the real question is whether the system will converge to a particular equilibrium point. Convergence means simply that a genetic system (described as a sequence in generation time) initiated at some point will move to the equilibrium point under consideration. It is not sufficient to prove that only one stable equilibrium exists as this does not imply convergence to that equilibrium if we have either simultaneous recurrence formulae, as in (2) below, or a recurrence formula of the second order, as in (3) below.

In this paper we confine ourselves to a di-allelic locus in a large random mating population. The system will be shown to converge to a stable equilibrium. This analysis can be adapted for an autosomal locus.

The basic equations: Denote the two alleles by A and a , and the viabilities of the genotypes AA , Aa and aa in the homogametic sex (assumed to be female for ease of reference) and of the genotypes A and a in the heterogametic sex (assumed to be male) by a, h, b, u and v respectively (these being positive constants). Let the ratio of the gene frequency of A to that of a be f for the females, and m for the males. We will denote the generation under consideration by a suitable subscript. Thus the relative frequencies of the genotypes in the $(N+1)$ th generation, at birth and at maturity (after selection) are given in the table below.

Stage	Females			Males	
	AA	Aa	aa	A	a
Birth	$f_N m_N$	$(f_N + m_N)$	1	f_N	1
Maturity	$af_N m_N$	$h(f_N + m_N)$	b	uf_N	v

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

$$m_{N+1} = \frac{u}{v} f_N$$

which leads to our basic recurrence relation,

$$f_{N+2} = \frac{2auf_N f_{N+1} + h(uf_N + vf_{N+1})}{2bv + h(uf_N + vf_{N+1})}. \quad (3)$$

Equilibrium: The condition for equilibrium is $f_N = f_{N+1} = \hat{f}$, say. Therefore

$$2auf^2 + h(uf + vf) = \hat{f}(2bv + h(uf + vf))$$

for equilibrium. This is satisfied by $\hat{f} = 0$ (i.e. $p=r=0$) and by $1/\hat{f} = 0$ (i.e. $q=s=0$). The only nondegenerate equilibrium (with both alleles present) is for

$$\hat{f} = (h^* - b^*)/(h^* - a^*) \quad (4)$$

where (MANDEL 1959)

$$au = a^*; \quad bv = b^*; \quad h(u + v)/2 = h^*. \quad (5)$$

From (4), since \hat{f} is a gene ratio and hence positive, either

- (i) $(h^* - b^*) > 0$ and $(h^* - a^*) > 0$
- or (ii) $(h^* - b^*) < 0$ and $(h^* - a^*) < 0$.

Convergence and stability: The condition $((h^* - a^*) > 0$ and hence $(h^* - b^*) > 0$) previously established as necessary and sufficient for the nontrivial equilibrium to be stable (EDWARDS 1961; KIMURA 1960) will be proved to be sufficient for convergence. Thus, if this condition is satisfied, convergence of the gene frequency to the nontrivial equilibrium is assured.

In outline, the proof is as follows. Under certain restrictions imposed on the original gene frequencies, the sequence of values of f from generation to generation, $\{f_N\}$, is shown to tend monotonically to the nontrivial equilibrium. It is then proved that any set of original gene frequencies will lead to a sequence bounded by two such monotonic sequences. Since the monotonic sequences converge to the nontrivial equilibrium, so does the general sequence. Previous authors have not considered the convergence of the system but have been concerned only with the nature of the equilibrium.

The case in which the condition is not fulfilled is considered in a similar manner. However, the absence of any nontrivial stable equilibrium does not ensure the convergence of the process to one of the trivial stable equilibria. CORMACK (1964) has shown that convergence to the nontrivial equilibrium is possible even though that equilibrium is not stable.

Proofs:

(i) Consider $(h^* - a^*) > 0$ and $(h^* - b^*) > 0$, and $f_0 = f_1 = \hat{f} = (h^* - b^*)/(h^* - a^*)$. Then since $f_0 \geq \hat{f} = (h^* - b^*)/(h^* - a^*)$, $(h^* - a^*) > 0$ and $(h^* - b^*) > 0$, $(h^* - a^*)f_0 \geq (h^* - b^*)$. Further, since $a^* > 0$ and $b^* > 0$, we have $h^*f_0 + b^* \geq a^*f_0 + h^*$, and so

$$f_0 \geq \frac{f_0(a^*f_0 + h^*)}{(b^* + h^*f_0)} = f_2.$$

(ii) We next note that if the equation (3) is written as

$$g(f_N, f_{N+1}) = f_{N+2},$$

then $g(f_N, f_{N+1})$ is a real function of two real variables f_N and f_{N+1} in the region

R, where f_N and $f_{N+1} > 0$, and $g(f_N, f_{N+1})$ has continuous partial derivatives of all orders with respect to f_N and f_{N+1} . In particular

$$\frac{\partial g(f_N, f_{N+1})}{\partial f_N} = \frac{4aubvf_{N+1} + 2auhv f_{N+1}^2 + 2hubv}{\{2bv + h(uf_N + vf_{N+1})\}^2}$$

which is positive in the region R. Similarly

$$\frac{\partial g(f_N, f_{N+1})}{\partial f_{N+1}} > 0 \text{ in R.}$$

(iii) Thus, by a Taylor expansion and the above arguments,

(iiia) if $f_1 \geq \hat{f}$ and $f_0 \geq \hat{f}$ then $\hat{f} = g(\hat{f}, \hat{f}) \leq g(f_0, f_1) = f_2$, and

(iiib) if $f_N \geq \hat{f}$ and $f_{N+1} \geq \hat{f}$ then $f_{N+2} = g(f_N, f_{N+1}) \geq g(\hat{f}, \hat{f}) = \hat{f}$.

Further (iiic) if $f_N \geq f_{N+1} \geq f_{N+2}$ then $f_{N+3} = g(f_{N+1}, f_{N+2}) \leq g(f_N, f_{N+1}) = f_{N+2}$.

(iv) The conditions from (i) and the relations of (iii) imply that the sequence $\{f_N\}$, where $f_0 = f_1 \geq \hat{f}$, is a monotonic decreasing sequence with exact lower bound $\hat{f} = (h^* - b^*)/(h^* - a^*)$. Since $\hat{f} > 0$ the sequence must converge to this value (Figure 1A).

Similar arguments lead to the result that for $(h^* - a^*) > 0$ and $f_0 = f_1 \leq \hat{f}$ then $\{f_N\}$ is a monotonic increasing sequence with exact upper bound \hat{f} and therefore converges to \hat{f} (Figure 1B).

(v) Consider a general sequence $\{f_N\}$ for which $f_0 \neq f_1$. Suppose $\{H_N\}$ and $\{K_N\}$ are two sequences defined by equation (3) and such that $K_0 > H_0$ and $K_1 > H_1$, then by arguments similar to those of (iii) we have that $K_N > H_N$ for all N . Thus if we have f_0 and f_1 , where $f_0 > f_1$ and we define $\{H_N\}$ and $\{K_N\}$ by $H_0 = H_1 = f_1$ and $K_0 = K_1 = f_0$ then for all N , $K_N > f_N > H_N$.

Sequences such as $\{H_N\}$ and $\{K_N\}$, with their first two members equal, have been shown to converge to \hat{f} . We now have that $\{f_N\}$ is bounded by above and below by $\{K_N\}$ and $\{H_N\}$ respectively, and since both $\{K_N\}$ and $\{H_N\}$ converge to

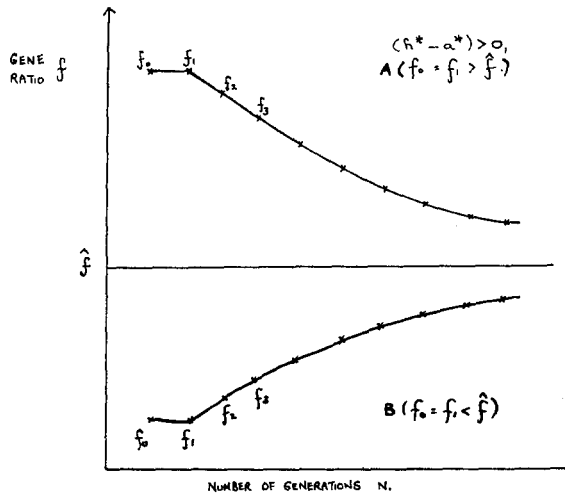


FIGURE 1.

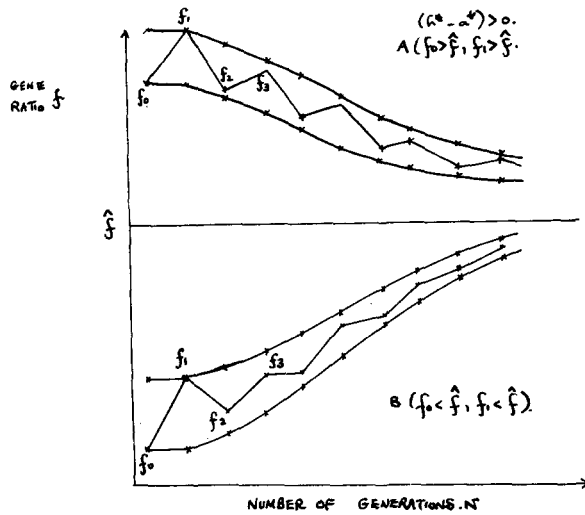


FIGURE 2.

\hat{f} then so does $\{f_N\}$ (Figures 2A, 2B and 3).

This concludes the proof that $(h^* - a^*) > 0$ is a sufficient condition for convergence.

A corollary of this result is that for $(h^* - a^*) > 0$ the nondegenerate equilibrium point is stable. Suppose we consider any perturbation from this equilibrium. This perturbation merely defines new values f_0 and f_1 with which to initiate a new sequence. The new sequence must converge to \hat{f} , and so stability is assured.

The investigation of the behaviour of the sequence $\{f_N\}$ when $(h^* - a^*) < 0$

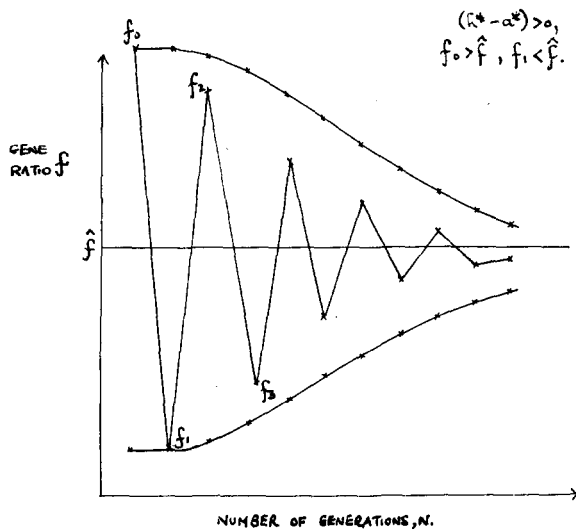


FIGURE 3.

follows similar lines. The results will be stated, proofs being exactly analogous to those given above.

(I) (a) If $f_0 = f_1 \leq \hat{f}$ then $f_2 \leq f_1 = f_0 \leq \bar{f}$.

(b) If $f_0 = f_1 \geq \hat{f}$ then $f_2 \geq f_1 = f_0 \geq \bar{f}$.

(II) (a) If $f_0 = f_1 \leq \hat{f}$ then $\{f_N\} \downarrow N$ and converges to zero.

(b) If $f_0 = f_1 \geq \hat{f}$ then $\{f_N\} \uparrow N$ and converges to infinity.

(iii) If sequences $\{f_N\}$, $\{H_N\}$ and $\{K_N\}$ have starting values f_0, f_1 ; f_0, f_0 ; f_1, f_1 ; then $\{f_N\}$ is bounded above, by either $\{K_N\}$ or $\{H_N\}$ and below, by the remaining sequence.

Here the similarity between the two cases ends.

If $f_0 \leq \hat{f}$ and $f_1 \leq \hat{f}$ then $\{f_N\}$ is bounded above and below by sequences both converging to zero and must also converge to zero (Figure 4B). Similarly if $f_0 \geq \hat{f}$ and $f_1 \geq \hat{f}$, $\{f_N\}$ is bounded above and below by sequences converging to infinity, and hence must also converge to infinity (Figure 4A).

However, if $f_0 \geq \hat{f}$ and $f_1 \leq \hat{f}$, $\{f_N\}$ is bounded above by an increasing sequence, and below by a decreasing sequence, and no definite conclusion about its convergence, or otherwise, can be reached.

A sufficient condition for $\{f_N\}$ to converge is that for some M f_M and f_{M+1} lie on the same side of \hat{f} . If both are below then $\{f_N\}$ converges to zero; if both are above then it converges to infinity.

This concludes the main results of the paper.

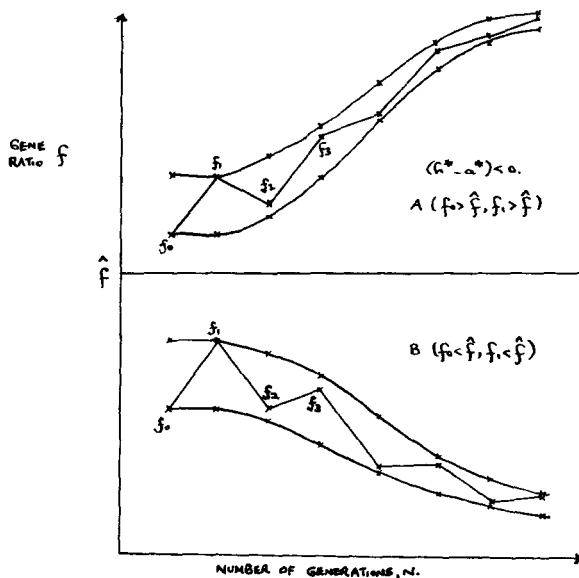


FIGURE 4.

A more general equation: The equations (2) are a particular case of a more general pair.

$$f_1 = \frac{2af_0m_0 + h(f_0 + m_0)}{2b + h(f_0 + m_0)}; \quad m_1 = g(f_1, m_0, f_0) \quad (6)$$

(i) $m_1 = (u/v) f_0$ is the special case considered above.

$$(ii) \text{ If } m_1 = \frac{2cf_0m_0 + k(f_0 + m_0)}{2d + k(f_0 + m_0)} \quad (7)$$

then we have the autosomal case with differential viabilities for the sexes.

(iii) If $m_1 = f_1$ we have the autosomal case without sex-differential viabilities.

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SUMMARY

A di-allelic sex-linked locus undergoing selection is considered. It is shown that only one nontrivial equilibrium exists, and the condition, under which convergence of the gene frequencies to this value is ensured, is established, and shown to be identical to that previously established for stability.

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