Sa and chestnut (Eddleman and Bell, 1963) had not changed. Thus it is probable that the *Sa* gene has not been involved in an inversion, at least of very great size.

The data clearly indicate the presence of a balanced lethal system in this species of flour beetles. In addition to being useful in genetic studies once sufficient genetic markers become available, the lethal gene also serves a useful immediate purpose. In order to maintain the *Sa* stock, it is necessary to select mutant individuals at frequent intervals. With the balanced lethal system present in the stock, it can be maintained for a considerable length of time without having to be selected. Furthermore, it might be possible to balance an *Fta* strain with the same lethal, particularly if it is located between *Sa* and *Fta*.

4. SUMMARY

A balanced lethal system is described in linkage group VII of the flour beetle, *Tribolium castaneum*. Short antenna (*Sa*), a dominant gene with recessive lethal effects is located from 0·5 to 3 units from an autosomal lethal.

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THE PROBABILITY OF SURVIVAL OF A NEW MUTANT IN A FLUCTUATING ENVIRONMENT

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1. INTRODUCTION

THE classical treatment of the problem of the probability of survival of a favourable new mutant has always supposed that the population in which the mutation occurs is of constant size. This may well be the most commonly occurring situation, but two other cases at least deserve some attention. These are, firstly, the case where the population size undergoes cyclic fluctuations, and secondly the case where the population size is initially small and then grows fairly rapidly until it reaches an equilibrium value, where it levels off. In this paper we derive survival probabilities under each of these circumstances.

2. CYCLIC POPULATION SIZE

It is convenient to use haploid population terminology, although this can readily be changed to diploid. Thus a mutant, in the diploid case, means a heterozygote having one mutant and one wild type allele and by offspring of a mutant we mean always such a heterozygote, wild type offspring not being of interest. We may ignore, in the diploid case, the formation of homozygous mutants, since these will occur with negligible frequency during the critical early generations after the initial mutant is born.

Consider a population whose size assumes the cyclic sequence of values $N_1, N_2, \ldots, N_k, N_1, N_2, \ldots$. At the locus in question some allele A is fixed in the population and at time zero a new mutant a appears, after which there is no further mutation. Suppose that the mutant produces $1+\delta$ offspring, on the average, for every one produced by the wild type. We wish to find the probability of eventual survival (*i.e.* fixation) of the new mutant. It is clear that this probability will depend on the size of the population when the mutation first appears, so that our analysis must derive a set of k survival probabilities, corresponding to the k possible initial population sizes.

Any mutant individual (*i.e.* not only the initial mutant but also its descendants) can be classified into one or other of k types $T_1, \ldots, T_k$, according to the rule that the individual is T_i if it exists at a generation when the population size is N_i. Writing $T_{k+1} = T_1$ for notational convenience it is clear that a T_i mutant can have only T_{i+1} offspring, and further that the mean number of such offspring is

$$(1+\delta)N_{i+1}/N_i \tag{2.1}$$

(We make the notational convention that $N_{k+1} = N_1$.) These considerations enable us to use immediately the mathematical results for multiple-type branching processes given by Harris (1963, pp. 40, 41, 46). In brief, the relevant results of Harris may be stated as follows. Let m_{ij} be the mean number of offspring of type T_j from a T_i parent, and let M be a matrix whose i-jth. element is m_{ij}. Then if the absolute value of the largest eigenvalue of M exceeds unity, the probability of survival of the mutant exceeds zero; if this largest eigenvalue is less than or equal to unity, the probability of survival is zero. In the former case, if S_i is the probability of extinction of the line initiated by a mutant which first appears when the population size is N_i, then the S_i $(i = 1, \ldots, k)$ are the unique positive solutions less than unity of the set of equations

$$S_i = f_i\,(S_1, \ldots, S_k) \quad (i = 1, \ldots, k) \tag{2.2}$$

The interpretation of $f_i\,(S_1, \ldots, S_k)$ is that the coefficient of $S_1^\alpha, S_2^\beta, \ldots S_k^\gamma$ in its Taylor expansion is the probability that a T_i parent has α offspring of type T_1 β of type T_2, ..., γ of type T_k: that is to say $f_i\,(S_1, \ldots, S_k)$ is the probability generating function of the offspring distribution from a T_i parent. Since, in our case, a T_i parent can have only T_{i+1} offspring, we may write (2.2) as

$$S_i = f_i\,(S_{i+1}) \tag{2.3}$$

where $S_{k+1} = S_1$. The functions $f_i\,(S)$ must satisfy, from (2.1) the requirement

$$f_i'\,(1) = (1+\delta)\,N_{i+1}/N_i \tag{2.4}$$

In the rest of this paper we shall assume, for convenience of exposition and for the purpose of obtaining numerical results, that all offspring distributions are Poisson. In this case equations (2.3) and (2.4) give

$$S_i = \exp -[(1+\delta)\ (N_{i+1}/N_i)\ (1-S_{i+1})] \tag{2.5}$$

or, in terms of survival probabilities $\pi_i = 1-S_i$,

$$-\log\ (1-\pi_i) = (1+\delta)\ (N_{i+1}/N_i)\ \pi_{i+1}\ (i = 1, \ldots, k) \tag{2.6}$$

Again we have $\pi_{k+1} = \pi_1$. Before solving (2.6) we must prove that the required survival probabilities are positive. The result of Harris quoted above assures us that this is the case if the largest eigenvalue of M, where

$$M = (1+\delta) \begin{Bmatrix} 0 & N_2/N_1 & 0 & 0 \ldots 0 \\ 0 & 0 & N_3/N_2 & 0 \ldots 0 \\ \cdots & \cdots & \cdots & \cdots \\ N_1/N_k & 0 & 0 & 0 \ldots 0 \end{Bmatrix}$$

exceeds unity in absolute value. Now the eigenvalues of M are easily shown to be

$$(1+\delta)\ \theta_j\ (j = 1, \ldots, k)$$

where the θ_j are the kth roots of unity, given by

$$\theta_j = \exp\ (2\pi ij/k),\ (j = 1, \ldots k),\ i^2 = -1$$

Since the absolute value of each θ_j is unity, all the eigenvalues have absolute value $1+\delta$ so the condition that survival probabilities exceed unity is $\delta > 0$.

The numerical solution of (2.6), while tedious, is straightforward, the following algorithm being applicable. Put $i = 1$ in (2·6) and choose a trial value for π_1. From (2·6) calculate π_2. Now put $i = 2$ in (2·6) and using the calculated value of π_2 calculate π_3, and so on. Eventually a value π_{k+1} is obtained from this process. If π_{k+1} exceeds the trial value π_1 then the latter is too large and a smaller value should be chosen; if π_{k+1} is less than π_1 the latter is too small. If $\pi_{k+1} = \pi_1$, then this is the required value and the remaining values $\pi_2, \ldots, \pi_k$ will also have been calculated. Such a procedure can lead to satisfactory values for the π_i after three or four iterations.

Numerical example. Consider a population whose size assumes the cyclic sequence of values N, $2N$, $4N$, $2N$, N, $2N$, . . .; that is for two consecutive generations the population size is doubled, then for two consecutive generations it is halved, after which the process starts again. If $\delta = 0{\cdot}01$, survival probabilities are positive and solve

$$2{\cdot}02\ \ \pi_2 = -\log\ (1-\pi_1), \quad 2{\cdot}02\ \ \pi_3 = -\log\ (1-\pi_2),$$

$$0{\cdot}505\ \pi_4 = -\log\ (1-\pi_3), \quad 0{\cdot}505\ \pi_1 = -\log\ (1-\pi_4).$$

We find

$$\pi_1 = 0{\cdot}0382,\ \pi_2 = 0{\cdot}0193,\ \pi_3 = 0{\cdot}0096,\ \pi_4 = 0{\cdot}0191.$$

When $\delta = 0{\cdot}1$ we find

$$\pi_1 = 0{\cdot}2985,\ \pi_2 = 0{\cdot}1612,\ \pi_3 = 0{\cdot}0799,\ \pi_4 = 0{\cdot}1514.$$

We note the strong dependence of survival probabilities on the size of the population when the mutation first occurs. Indeed, survival probabilities

seem to be roughly proportional to the inverse of the population size when the mutation occurs; we now show when δ is small (not larger than about 0·05), k moderate (not larger than 5 or 10) and the N_i not too different, that this is a general result.

Putting $(1+\delta)^{-1}\, N_i/N_{i+1} = R_i$, we get from (2.6) (ignoring terms of order π_i^3),

$$\pi_{i+1} = R_i\,(\pi_i + \tfrac{1}{2}\pi_i^2). \tag{2.7}$$

Similarly

$$\begin{aligned}\pi_{i+2} &= R_{i+1}(\pi_{i+1} + \tfrac{1}{2}\pi_{i+1}^2).\\ &= R_{i+1}\,R_i\,\pi_i + \tfrac{1}{2}[R_i\,R_{i+1} + R_1^2\,R_{i+1}]\,\pi_1^2.\end{aligned} \tag{2.8}$$

Continuing this process we find

$$\begin{aligned}\pi_{i+j} &= R_{i+j-1} \ldots R_i\,\pi_i + \tfrac{1}{2}[R_i \ldots R_{i+j-1}\\ &+ R_i^2\,R_{i+1} \ldots R_{i+j-1} + \ldots (R_i \ldots R_{i+j-2})^2 \times R_{i+j-1}]\,\pi_i^2.\end{aligned} \tag{2.9}$$

Now $\pi_{i+k} = \pi_i$, so that to the order of accuracy considered

$$\begin{aligned}\pi_i = 2[1 - R_{i+k-1} \ldots R_i][R_i \ldots R_{i+k-1} + R_i^2 \ldots R_{i+k-1}\\ + \ldots + (R_i \ldots R_{1+k-2})^2\,R_{i+k-1}]^{-1}.\end{aligned} \tag{2.10}$$

Now
$$\begin{aligned}R_i \ldots R_{i+k-1} &= (1+\delta)^{-k}\\ &\simeq 1 - k\delta,\end{aligned}$$

so that from (2.10)

$$\pi_i \simeq 2N_i^{-1}\,k\delta(N_{i+1}^{-1} + \ldots + N_{i+k-1}^{-1})^{-1}$$

If we define the harmonic mean N^* of the population sizes by

$$kN^{*-1} = N_1^{-1} + \ldots + N_k^{-1},$$

we have finally,

$$\pi_i \simeq 2\delta N^*/N_i. \tag{2.11}$$

We note that π_i is thus, to this order of approximation, inversely proportional to N_i, verifying our previous observation.

It is reasonable to assume that any mutation which occurs during any given cycle will occur when the population size is N_i with probability $N_i/(N_1 + \ldots + N_k)$. In this case the weighted survival probability $\pi = (\sum \pi_i N_i)/(\sum N_i)$ becomes

$$\pi = 2\delta N^*/\bar{N},$$

where $\bar{N} = (N_1 + \ldots + N_k)/k$. For given $\bar{N}$ and k, this weighted value is maximized when the N_i are equal, where it assumes the value 2δ; when the N_i differ considerably the value may be considerably less than 2δ. Thus we conclude that constancy of population size is a favourable condition for survival of new mutants.

3. INCREASING POPULATION SIZE

We consider in this section the case where the population size increases during early generations and then levels off at a stable value; to be definite we suppose that the population size assumes the sequence of values N_1, N_2, ..., N_{k-1}, N_k, N_k, N_k, ... Here we are thinking mainly of the case

where $N_1 > N_{i-1}$, although the subsequent analysis is quite general. Let the mutation first occur when the population size is N_1. Here we can classify a mutant into one or other of k types $T_1, \ldots, T_k$, where a T_i mutant is born into a population of size N_i. Now a T_i mutant ($i = 1, 2 \ldots k-1$) can give birth only to T_{i+1} offspring, while a T_k mutant can give birth only to T_k offspring. If we suppose that a mutant produces $1+\delta$ offspring, on the average, for every one of the wild type, then the matrix M (see previous section) is of the form

$$M = (1+\delta) \begin{Bmatrix} 0 & N_2/N_1 & 0 & 0 & \ldots\ 0 \\ 0 & 0 & N_3/N_2 & 0 & \ldots\ 0 \\ 0 & 0 & 0 & N_4/N_3 & \ldots\ 0 \\ . & . & . & . & . \\ 0 & 0 & 0 & 0 & \ldots\ 1 \end{Bmatrix}$$

The only no-zero eigenvalue of this matrix is $(1+\delta)$; thus $\delta > 0$ is again the necessary and sufficient condition that survival probabilities are positive. In this case, if S_i is the probability of eventual extinction of the line initiated by a single new mutant born when the population size is N_i, then the S_i are the unique positive solutions (less than unity) of the set of equations

$$S_i = \exp -[(1+\delta)(N_{i+1}/N_i)(1-S_{i+1})], \ (i = 1, \ldots k-1) \qquad (3.1)$$

$$S_k = \exp -[(1+\delta)(1-S_k)] \qquad (3.2)$$

These equations are best solved by solving (3.2) for S_k, using (3.1) with $i = k-1$ to find S_{k-1} and so on, working back to S_1. In this case an iterative procedure is not required.

Numerical example: Consider a population which assumes the sequence of sizes, N, $2N$, $4N$, $8N$, $8N$, $8N$, ..., and for which $\delta = 0{\cdot}1$. Then using (3.2), π_4 solves

$$-\log (1-\pi_4) = 1{\cdot}1\ \pi_4,$$

so that

$$\pi_4 = 0{\cdot}1761.$$

Using (3.1) with $i = k-1$,

$$-\log (1-\pi_3) = 2{\cdot}2\ (0{\cdot}1761)$$

so that

$$\pi_3 = 0{\cdot}3212.$$

Similarly

$$\pi_2 = 0{\cdot}5067,$$
$$\pi_1 = 0{\cdot}6720.$$

Clearly a mutant born in generation 1 has a substantial chance of survival, due mainly to the subsequent increase in population size. In this respect it is interesting to note that had the population size increased immediately from N to $8N$, the probability of survival of a mutant born in generation 1 would solve

$$-\log (1-\pi_1) = 8{\cdot}8\ (0{\cdot}1761)$$

that is

$$\pi_1 = 0{\cdot}7877.$$

This is somewhat larger than the corresponding probability when the increase in size requires three generations. A further observation is that

had the population size doubled itself for a considerable number of generations, the probability of survival of a mutant born at the beginning of the process would be close to the solution of

$$-\log (1-\pi_1) = 2{\cdot}2\ \pi_1,$$

namely

$$\pi_1 = 0{\cdot}8437.$$

The above remarks make it clear that the substantial determinant of the fate of a new mutant is the absolute change in numbers of the mutant rather than the relative changes in frequency compared to the wild type. It is, of course, for this reason that all classical results have assumed stable population sizes.

A final remark might be made about the fate of an unfavourable new mutant. Taking the situation of the numerical case given above as an example, if the fitness of the new mutant is between 0·5 and 1 there will be a tendency for the mutant to increase in numbers during the generations when the population size is doubling; however as soon as the size stabilises such mutants will soon die out. For example, a mutant with fitness 0·75 born in the first generation has probability 0·6438 of having descendants in the fourth generation; in a stable population the corresponding probability is only 0·1564. Thus while the population size increases we should expect that a variety of new and perhaps unusual types would appear, to disappear again fairly soon after the population size stabilises.

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CHIASMA FREQUENCIES IN EUCHROMATIC AND HETEROCHROMATIC CHROMOSOMES

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1. INTRODUCTION

THE interrelationships of chiasma frequencies in euchromatic bivalents in the presence of extra euchromatin and heterochromatin have been described (Shah, 1964, 1965). In the normal diploid there was an indication of negative correlation in the standard bivalents while the addition of different numbers of supernumerary chromosomes was associated with a non-linear change in the character studied. In the present studies, the interrelationships between the standard chromosomes and the heterochromatic supernumerary chromosomes in plants with 2, 3 and 4 supernumerary chromosomes and in an asynaptic plant with two supernumeraries are presented.

2. MATERIAL AND METHODS

The plants used belong to *Dactylis glomerata* subsp. *lusitanica* ($2n = 14+$B's). All the plants having 2 and 4 supernumeraries, except the asynaptic plant, are sibs obtained from a cross of a diploid with no supernumerary and plant No. 7 (see table 1) and the reciprocal cross.

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