

On Defining the Sufficient Causes
for Natural Selection to Occur

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ABSTRACT. This paper examines the problem of defining the sufficient causes for natural selection to occur. An analysis of the optimal body size for a semelparous organism is used to illustrate the difficulty. It is suggested that no general set of conditions that are useful can be given. The analysis also indicates that shifts in the optimal value of a character can occur as a result of changes in life history parameters not directly related to that character.

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Natural selection is the central paradigm of modern theories in ecology and evolution. It is, therefore, important to be able to define precisely the circumstances in which it will occur. Verbal definitions of selection generally stress the importance of differences in survival or reproduction. For example, 'the essence of selection is that the carriers of different genotypes in a population contribute differentially, to the gene pool of the succeeding generations', (Dobzhansky 1951) or, 'natural selection operates through any factor that contributes to differential reproduction', (Mayr 1970) or, 'for any natural selection to occur at all, the processes must diminish the probabilities of survival to a different extent for various genotypes present in the population' (Roughgarden 1971). The first two definitions are difficult to express mathematically because the word 'differential' is ambiguous; the word may apply to either relative or absolute differences. Suppose, for example, the survival rates of two genotypes are reduced by some fraction; the relative survival rates remain the same but the absolute difference between them changes. The third definition is more explicit and suggests that a change in survival that is proportionally the same for all genotypes will have no effect. When there exists some genetical model for the character under consideration the problem of defining selection is relatively simple: since selection may then be described as 'any process that alters gene frequency in a directed fashion without change of the genetic material (mutation) or introduction from without (immigration)', (Wright 1969) it is only necessary to analyse the behaviour of the model when fitness values are assigned to the various genes or gene combinations. However, for most ecological studies no adequate genetic model exists and natural selection is assumed to be a process that optimizes some measure of fitness such as the malthusian parameter, r . That there may be circumstances in which optimization may not occur (Levins 1970, Turner 1970, Roff 1975) does not detract from the general utility of this assumption in organising a large body of ecological observations and in suggesting fruitful avenues of investigation.

The concept of optimization has been central to the study of variation in body size, as is attested by the frequent use of such words as 'adaptive variation' (Nevo 1973), 'adaptive significance' (Hamilton 1961, Grant 1965) 'adaptation' (Jameson *et al.* 1970), 'adaptive nature' (Price 1972) in the title of the paper. It is thus pertinent to ask if any of three definitions

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quoted above are sufficient to define the circumstances in which natural selection will cause a shift in the optimal body size. I shall consider this question with respect to the problem of finding the optimal body size of a semelparous organism.

Our first requirement is a definition of fitness. This is by no means a simple task. The most commonly used measure of fitness is the malthusian parameter, r (Fisher 1958). However, in a stochastic world persistence and maximizing the average value of r may not be identical strategies (Murphy 1968, Gadgil and Bossert 1970, Roff 1974, 1978, Fairbairn 1977). Furthermore, if a long time horizon is used fitness measures that concentrate on patterns of energy flow through a community may be most appropriate (Van Valen 1976). However, for the purposes of this paper I shall adopt r as a measure. To obtain r we must solve the equation

$$\sum_x \exp(-rx) l_x m_x = 1 \quad (1)$$

where x is age, l_x is the survival to age x and m_x is the number of female offspring produced at age x . For a semelparous organism in which the breeding period is short this equation reduces to

$$\exp(-rT) l_T m_T = 1 \quad (2)$$

and hence

$$r = \frac{\ln(l_T m_T)}{T}$$

where T is the generation length.

Within any given population it would seem reasonable to suppose that the size at maturity increases with the length of the immature stage: this is true for some insects (Robertson 1960, Kamm 1972, Masaki 1967, 1972) and Atlantic salmon (Schaffer and Elson 1975) and is probably a common (though not necessarily universal) phenomenon in poikilotherms. It has also been shown that in poikilotherms fecundity increases with body size (Chiang and Hodson 1950, Green 1956, Bagenal 1966, Spight 1976). These two factors operate in opposition, r decreasing with development time per se but increasing with fecundity. Because of the relationship between fecundity and development time (due to their mutual dependence on size at maturity) there should exist, in general, some intermediate body size at which r is maximized. We might expect this optimum body size to depend also upon the age schedule of survival. The duration spent in some life stages, such as the egg phase, is probably more or less independent of the final size of the animal, whereas the time spent in another stanza, such as the larval period, will almost certainly influence of the final size. In the first case a simple survival probability, say p , may be applied to all genotypes; in the second, a survival function that is dependent on time or size must be applied. The case I shall consider is that in which, for each life stanza, other than the egg stage, the instantaneous rate of mortality remains constant, i.e. the probability of surviving some small increment of time does not depend on size. This assumption generates a

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Type II survival curve (Pearl 1928) and is one generally made for fish (Ricker 1975). As mentioned, each life stage may have a characteristic mortality rate but in the present case, I shall assume a common value, M . The proportion of animals surviving to reproduce is thus the product of two types of mortality, a constant factor, p and a time dependent factor, e^{-MT} .

The optimum body size can be found from equation (3) as follows: let the relationship between sizes and development time be $D(S)$, ($T = D(S)$), and between fecundity and size be $F(S)$, ($m_T = F(S)$). Then

$$\begin{aligned} r &= \frac{\ln(pF(S)e^{-MD(S)})}{D(S)} \\ &= \frac{\ln(pF(S))}{D(S)} - M \end{aligned} \quad (4)$$

r is maximized when dr/ds equals 0, (and $d^2r/ds^2 < 0$), i.e. when

$$F'(s)D(S) - F(S)D'(S)\ln[pF(S)] = 0, \text{ provided } F(S)D(S)^2 > 0 \quad (5)$$

where $F'(S)$ and $D'(S)$ are the derivatives of $F(S)$ and $D(S)$ respectively.

The first point to note about equation (5) is that it does not involve M and hence the optimal size is independent of M . But a change in M changes the relative mortalities. For example, suppose there exist two genotypes with generation lengths 1 and 2 weeks: the proportion of the second genotype surviving relative to the first is e^{-M} ($\exp(-M)/\exp(-2M)$). Clearly, as M increases relatively fewer of the second type survive. Thus we have a situation in which a differential change in the survival rates of genotypes does not change the optimal genotype. This curious result means that it is possible, under the conditions given above, to increase the fishing mortality of some semelparous fish, such as salmon, and yet have no effect on the age of first reproduction.

The second point to note is that equation (5) does involve p and hence the optimal genotype is shifted by a change in p even though all genotypes are equally affected. In general, $F(S)$, $D(S)$ and their derivatives will be increasing functions of body size and, therefore, a decrease in p leads to an increase in the optimal body size: for example, a reduction in fertility favours an increase in size.

These two apparently paradoxical results can be understood by examining equation (4); r is a linear function of M but a non-linear function of p . Thus a change in M changes r by the same amount for all genotypes but a change in p has a differential effect on r , thereby shifting the maximum. The independence of the optimal body size from the time dependent mortality function (in this case e^{-MT}) is not a universal phenomenon since most functions will enter equation (4) as nonlinear components. Similarly, if breeding is spread over a significant period of time equation (2) is inappropriate and an equation involving a series of terms, as in equation (1) is required and this introduces even the survival function e^{-MT} into the

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solution as a non-linear term. The factor p , however, always enters the equations as a non-linear term and hence this result is general. Although the independence of the optimal body size from M may not be generally true the above analysis suggests that changes in p may be more significant in causing shifts in the optimal body size than changes in the relative survival rates.

While the case outlined above is extreme the analysis does point out the difficulty of defining the sufficient causes for natural selection to occur. The condition given by Roughgarden (1971) is insufficient since it implies that changes in p will not cause any genetic changes. The conditions given by Dobzhansky (1951) or Mayr (1970) are incorrect in the example given above because changes in the relative survival rates (M) may not cause genetic shifts. The message of the above analysis is that the definition of sufficient cause for natural selection to occur may only be made explicit for a well defined circumstance and may change with the circumstance. For this reason the best we can say of the general situation is;

(1) If there is variation in the survival rates of different genotypes, then all other things being equal, there will exist some genotype that is the most fit.

(2) Changes in the survival rates may or may not lead to changes in the 'most fit' genotype.

Defining the most fit genotype may not, unfortunately, be a simple matter and in some cases the genotype that survives may not be that which is 'ecologically' optimal. However, the assumption of some ecological optimum phenotype (and hence genotype) may be a useful heuristic rule, if nothing else, and is therefore worthwhile retaining. Given such rules it is possible to define the optimal phenotype and hence examine the effects of variation in survival rates, making no a priori presumptions concerning the selective effects of such variation. After such an examination it is then possible to state the sufficient conditions for natural selection to occur.

Another interesting fact demonstrated by the above model is that natural selection can act on a character even when the actual shifts in survival do not directly influence that character. For example, a reduction in the proportion of eggs hatching may cause a shift in the optimum body size. In this respect it is significant that gradients in body size, observed in both homeotherms (McNab 1971, James 1970) and poikilotherms (Ruibal 1957, David and Boquet 1975), have generally been explained as a result of selection for body size per se (Scholander 1955, James 1970, Nevo 1973, Kendeigh 1976), (although for a rather different approach see Case 1978). While selection may act directly on body size there may also be a significant effect via changes in other life history parameters: it would indeed be strange if along some latitudinal gradient there were not shifts in most or all of the survival and age specific reproduction rates. Thus any explanation of body size or other characteristic must consider all variations in life history components, not just those that are directly linked to the character under study.

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