NOTES AND COMMENTS

A NOTE ON APOSTASY

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CLARKE (1962*a* and *b*) has suggested that frequency-dependent apostatic selection by predators may be an important factor in maintaining the striking visual polymorphisms found in several species of animals, especially the snails *Cepæa nemoralis* and *C. hortensis*. More recently, Clarke and O'Donald (1964) and Clarke (1964) have investigated the general properties of this type of system mathematically, pointing out that although they may be of rather wide applicability, situations in which selective values vary with frequency have so far received little attention. The paper by Haldane and Jayakar (1963) may be added to those which they cite.

The treatment presented here arose from the need for a formal model for apostatic selection in connection with an experimental investigation of its effects. The experiments were carried out by Mr F. H. Pough at Amherst College, using Chickadees (*Paridæ*) as predators and coloured sunflower seeds as the "polymorphic" prey. The results he obtained were not conclusive, but it is hoped to continue work along these lines. The present method appears to permit an easier interpretation of experimental data than that of Clarke and O'Donald. Using it, their general conclusions can be obtained, but a new conclusion is also drawn which may be relevant to the situation in *Cepæa*.

1. THE SELECTIVE COEFFICIENT

In order to predict the theoretical consequence of differential predation due to development of searching image by a predator it is necessary to find a function which will describe the relation between the frequency with which a form is eaten and the frequency which was available.

Suppose the prey population consists of two colour forms, say blue and green. Let

L = initial frequency of blue

M = initial frequency of green = $1 - L$

I = fraction of the population eaten by a predator; of which a fraction G was blue and H ($= 1 - G$) was green.

Then $\frac{GI}{L}$ is the predation on blue expressed as a fraction of the initial quantity available, and $\frac{HI}{M}$ is the predation on green. These quantities must take values between 0 and 1, since $GI \leq L$ and $HI \leq M$. Consequently,

$u = 1 - \frac{GI}{L}$ = blues surviving as a fraction of the original quantity and

$v = 1 - \frac{HI}{M}$ = fraction of green surviving.

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Now suppose that the selective coefficient of the green morph at any given frequency is the variable function, s , while the selective coefficient of blue is zero. Then

$$L: (1-s)M = Lu : Mv$$

$$s = 1 - \frac{v}{u} = \frac{I(H-M)}{M(L-GI)} \quad (1)$$

Since the selective effect depends only on external appearances this expression holds true whether the forms are distinct species or dominant or recessive morphs, although it is not a sufficient requirement for co-existence of both species in the first case.

The theory supposes that development of searching image by the predator will lead to the following type of relation between H and M (cf. data figured by Clarke, 1962*a*).

The selective coefficient, s , can then be found from this relation. About the point $H = M$, which is the equilibrium point, the observed regression may for convenience be taken to be approximately linear, so that $H = bM + c$, b and c being determined empirically.

2. INTERACTION INVOLVING TWO SPECIES

If L and M are the frequencies of two distinct but similar species, and if we assume that the species could coexist, the new frequency after a selective event is

$$M_1 = \frac{(1-s)M_0}{L_0 + (1-s)M_0}.$$

Then
$$\Delta M = M_{t+1} - M_t = \frac{-sLM}{1-sM}, \quad (2)$$

is the change in frequency brought about by selection. Assuming the linear relationship to hold near the equilibrium point and substituting for s ,

$$\Delta M = \frac{I(M-bM-c)}{1-I}. \quad (3)$$

Equilibrium occurs when $\Delta M = 0$, and its nature may be found by determining the slope of the line about the equilibrium frequency (Lewontin, 1958) from the equation:

$$\frac{d\Delta M}{dM} = \frac{I(1-b)}{1-I}. \quad (4)$$

It is clear that the outcome depends not only on the observed relation between H and M , but also on the intensity of predation.

3. POLYMORPHISM WITH DOMINANCE

Let $M = q^2$ = initial frequency of the recessive phenotype, and $L = 1 - q^2$. Then s is the selective coefficient of the recessive morph. By analogy with (2) we have the usual equation,

$$\Delta q = \frac{-sq^2(1-q)}{1-sq^2}. \quad (5)$$

If the linear relationship holds:

$$\Delta q = \frac{I(1-q)(q^2-bq^2-c)}{(1-I)(1-q^2)} \quad (6)$$

which is at an equilibrium when $q = \sqrt{\frac{c}{1-b}}$ and $b > 1$. Then

$$\frac{d\Delta q}{dq} = \frac{I[q(1-b)(2-3q+q^3)+c(1-q^2)]}{(1-I)(1-q^2)^2} \quad (7)$$

gives the slope about the equilibrium point. By making suitable adjustments to c one may obtain a series of curves of b on I similar to those given by expression (4). There will be a stable equilibrium for small values of b and I ; but if I exceeds about 0.4 the likelihood of oscillation in frequency becomes quite large.

4. BALANCE BETWEEN APOSTASIS AND OTHER SELECTION

In practice it is unlikely that the two forms will ever be equivalent with respect to the effect of other selective agents. If one of them is at a disadvantage due to a constant selective pressure then a balance may be attained between apostasis and the other factor.

Suppose that frequency-independent selection, with selective coefficient t , is sustained by the recessive morph. The outcome of the two agents acting simultaneously in one generation will be,

$$\Delta q = -\frac{sq^2(1-q)}{1-sq^2} - \frac{tq^2(1-q)}{1-tq^2}.$$

At low frequencies terms in q higher than q^3 may be ignored, so that this equation is rewritten,

$$\Delta q = \frac{-q^2(1-q)(s+t)}{1-q^2(s+t)} \quad (8)$$

$\Delta q = 0$ when $s = -t$, at which point:

$$\frac{d\Delta q}{dq} = \frac{-2q(s+t)}{(1-tq^2-sq^2)^2} \text{ approximately.}$$

In general, the result of the interaction between s and t will be to reduce the slope of Δq on q at the equilibrium point. It will certainly shift the equilibrium frequency, but it is also possible that the resultant line will have a zero or negative slope throughout, so that no non-trivial equilibrium exists. The circumstances required to prevent this outcome may be found approximately by assuming that at very low frequencies of q , $H = bq^2$, where $1 > b \geq 0$. In practice one would certainly be unable to determine whether or not the regression was curved in this region. Then from equation (1) we can find,

$$s = \frac{-I(1-b)}{1-I-q^2(1-Ib)}.$$

Consequently, if q is assumed to be small enough for q^2 to be ignored, polymorphism may be expected provided

$$t < \frac{I(1-b)}{1-I}.$$

If $b = 0$ at this extreme, as it might do in practice, then

$$t < \frac{I}{1-I}.$$

At very high frequencies a similar approximation can be made, *i.e.* that $1-H = b(1-q^2)$. If b is assumed to be zero, or nearly so, $H \simeq 1$. Consequently, from (1),

$$s = \frac{I}{q^2}.$$

In this region both alleles will be retained in the population provided $t < -I$ approximately. The necessary condition for polymorphism, therefore, is that t should lie between $\frac{I}{1-I}$ and $-I$. Similarly, when t is the coefficient of a dominant gene the polymorphism will be retained provided it lies between $\frac{I}{(1-I)^2}$ and $-I(1-I)$.

5. SAMPLING ERROR

It seems probable that the low values of b and I , which are most likely to occur in a natural situation, will be accompanied by considerable sampling error effects. In a medium-sized population of, for example, a

few thousand, predators eat several hundred or fewer individuals. Examination of the first few dozens of these must determine their response to all the other potential prey that they come across. If, in a given generation, the gene frequency is q the samples taken by predators will be distributed about q with variance $\frac{q(1-q)}{2n}$, where n is the number required to allow

formation of a searching image. A large variance necessarily follows from the requirement that n should be small for apostasis to be effective. The size of the error would be modified if the predators acted successively so that each one influenced the frequency available to the next, or if n varied from one predator to another, but it is not likely to be reduced. Consequently, accidental variation in the response of the predators will add greatly to the indeterminacy of the system. This is especially true at gene frequencies near the middle of the range, where the variance is large and, if other selective agents are also operating, the regression of Δq on q can have a rather shallow gradient. It will be less important where s has large values and apostasis leads to a slope of Δq on q which is relatively steep compared with that derived from other types of selection. These circumstances occur at high or low gene frequencies. As a result, apostasis appears to be an effective agent preventing loss of morphs from a population due to adverse selection of other types against them, but would be relatively inefficient in defining the equilibrium frequency to which they tend.

6. SUMMARY

A method is suggested for the treatment of experiments on apostatic selection. The conditions leading to a stable equilibrium and to oscillations in gene frequency are shown, and the result of simultaneous frequency-dependent and frequency-independent selection is examined. Under simplified conditions a polymorphism will be retained in a population provided the fraction of individuals eaten by predators has about the same order of magnitude as the frequency-independent selective coefficient. The two types of selection acting together will tend to make the approach to equilibrium slow: and the sampling variance on the part of predators is likely to be large. Consequently, we should predict that if there was appreciable apostatic selection acting on populations of a polymorphic species, they would remain polymorphic but would show a wide range of gene frequencies.

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7. REFERENCES

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FRANCIS GALTON'S DERIVATION OF MENDELIAN RATIOS IN 1875

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It is generally believed that before 1900 no one apart from Mendel suspected that the frequencies of the various classes in the F₂ generation might approximate to simple ratios. It is, therefore, surprising to find that this is not the case, for in a letter which Francis Galton (1822-1911) wrote to his cousin Charles Darwin he derived the 1 : 2 : 1 ratio deductively reasoning from the premise that inheritance is due to a finite number of persistent particles. This letter, dated 18th December 1875, is preserved in the collection of Darwin Manuscripts at the University Library, Cambridge (Darwin MS. 105 (92, 93)) and a portion of it is reproduced here (plate I). It has already been published by the late Professor Karl Pearson in volume II of his biography of Galton (Pearson, 1914-30, pp. 189-190); but as it does not appear to be generally known it is well worth describing afresh.

The letter forms part of the correspondence between Galton and Darwin over the latter's hypothesis of pangenesis, the central idea of which was that every cell of the body gives off "minute granules or atoms" which he termed "gemmules". These gemmules congregate in the reproductive organs where they form the hereditary material of the germ cells. Galton did not deny the existence of these gemmules but he refused to believe that "they circulate freely throughout the system" (Darwin, 1868). Consequently he could not see how the hereditary material of the germ cells can possibly be derived from the somatic tissues.

In December 1875 Darwin wrote to Galton asking him how, on his view, it was possible to explain the fact that a hybrid may have every part of the stem, leaf and flower intermediate and will produce millions of buds all of which reproduce exactly this intermediacy. In his very interesting reply Galton deduced Mendelian ratios. It reads as follows:

42 RUTLAND GATE
Dec 19/75

My dear Darwin,

The explanation of what you propose does not seem to me in any way different on my theory, to what it would be in any theory of organic units. It would be this:—

Let us deal with a single quality, for clearness of explanation, and suppose that in some particular plant or animal and in some particular structure, the hybrid