

NOTES AND COMMENTS

EXPLORING APOSTATIC SELECTION

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1. INTRODUCTION

IN apostatic selection the forms which stand out from the norm by virtue of their rarity are at a selective advantage (Clarke, 1962). Such selection results from predators learning the appearance of commoner forms more readily than that of rarer forms (Clarke, 1962; Popham, 1941; Tinbergen, 1960; Allen and Clarke, 1968). We consider here a possible model for apostatic selection and how evidence for it may be analysed. We restrict discussion to dimorphic prey.

2. THE MODEL

If two morphs are exposed at densities D_1 and D_2 , if N_1 and N_2 are taken by the predator, and if there is no apostatic selection, then

$$N_1 = D_1 V_1 \quad \text{and} \quad N_2 = D_2 V_2 \quad (1)$$

where the constants V_1 and V_2 are measures of the visibilities of the two morphs.

We define:

$$N = N_1/N_2$$

$$D = D_1/D_2$$

$$V = V_1/V_2$$

and, following Cook (1965):

$$H = N_2/(N_1 + N_2)$$

$$M = D_2/(D_1 + D_2).$$

Then, equations (1) imply that:

$$H = \frac{M}{M + V(1 - M)} \quad (2)$$

and

$$N = DV. \quad (3)$$

(Equations (2) and (3) remain the same if one allows for the time taken to handle each prey item in equations (1).)

Since there will be equilibrium only when $H = M$ (and $N = D$), equations (2) and (3) each imply the eventual extinction of the more visible morph. If apostatic selection occurs there will be departure from (2) and

(3) and a non-trivial equilibrium point (since, however relatively visible is one of morphs, there can always be a relative density so low that its apparent density is lower than that of the other morph). To find a possible form for the relation under apostatic selection, we consider the function:

$$N = f(DV).$$

This must be of such a form that N/DV increases as DV increases, and is unity when DV is unity. It is unlikely that predators behave in such a way that the function is asymmetrical, so we also require that

$$\frac{1}{N} = f\left(\frac{1}{DV}\right).$$

The simplest function satisfying these conditions is

$$N = (DV)^b \tag{4}$$

for some constant $b > 1$. The equation corresponding to (2) is then:

$$H = \frac{M^b}{M^b + V^b(1-M)^b}. \tag{5}$$

As in all forms of frequency dependent selection, an equilibrium occurs when the fitnesses of the two morphs are identical, *i.e.* when

$$N = D = V^{\left(\frac{b}{1-b}\right)}$$

and

$$H = M = \frac{1}{1 + V^{\left(\frac{b}{1-b}\right)}}.$$

The slopes dN/dD and dH/dM at those points are both b .

3. FORMS OF ANALYSIS

Suppose that a set of observations of N_1 , N_2 and D is available and one wishes to estimate b and V . Note that if we set $x = \log_e D$, $P = H$, $\alpha = -b \log_e V$, and $\beta = -b$, (5) becomes the well-known logit function used in bioassay:

$$P = \frac{1}{1 + e^{-(\alpha + \beta x)}}.$$

Estimation of α and β can be carried out using the iterative maximum likelihood procedures described by Finney (1964). If there are more than two experimental values of D , a χ^2 test of homogeneity can be used to test the adequacy of the model.

For a simpler approximate method, a logarithmic transformation of (4) gives

$$\log N = b \log V + b \log D.$$

A straight line may be fitted to the transformed data by linear regression analysis. Since the variance of the $\log N$ is larger for extreme values of N than for moderate values, this is not strictly valid but the procedure is probably adequate unless many of the values of N are close to zero or infinity.

In general, the homogeneity test statistic calculated from the regression expected values will be larger than that from the logit analysis, so non-significance of the former implies that of the latter.

4. FITTING THE MODEL TO DATA

Popham (1941) exposed dimorphic populations of the bug *Sigara distincta* Fieb. to predation by Rudd (*Scardinius eryophthalmus* L.) in an aquarium. The populations differed in the relative densities of the two morphs offered (D) but the total densities of bugs and the background were the same in all (i.e. $(D_1 + D_2)$ and V were constant). As bugs were eaten, they were replaced, to keep both relative and total densities constant.

In fig. 1 the relative numbers of the two morphs eaten are plotted against the relative numbers available. The lines fitted to them are those estimated (a) by logit analysis ($b = 1.42$, $V = 2.15$) and (b) by linear regression ($b = 1.44$, $V = 2.20$). There is a close fit of the lines to the data and the regression homogeneity χ^2 is 3.48 (logit analysis: $\chi^2 = 3.30$) for two degrees of freedom, which is not significant. Thus the model is an adequate description of the data.

The value of b is significantly greater than one ($P < 0.05$), showing that the Rudd were selecting apostatically.

5. DISCUSSION

The model presented is the simplest mathematical description of apostatic selection. It does not claim to be a precise analytical description of predator behaviour. However, it does fit the data available with some precision, so it is probably reasonably close to such a description, though more data are needed to confirm this. It also provides an easy, but statistically valid, means of testing for evidence of apostatic selection.

Tinbergen's (1960) "searching image" hypothesis has led to the belief that a predator faced with polymorphic prey will concentrate almost completely on one morph—the morph which is the commonest among the first few individuals of the prey which the predator takes. If this is correct there will be a wide variation in the selection imposed by individual predators on the same population. "As a result, apostasis appears to be an effective agent preventing loss of morphs from a population . . . but would be relatively inefficient in defining the equilibrium to which they tend" (Cook, 1965). However, the data for the Rudd show very little variance about the theoretical line, even though they concern only three Rudd. It seems that, in this species at least, the individual reacts with sufficient precision to the relative densities of the morphs for apostasis to be capable of playing a much more exact role in governing polymorphisms than has often been allowed.

6. SUMMARY

1. The mathematically simplest description of apostatic selection is that the relative numbers of two morphs taken by a predator are some power of the apparent relative numbers available.

2. From the model follow two methods of estimating the value of the apostatic power function and of the relative visibility of the morphs, given certain data.

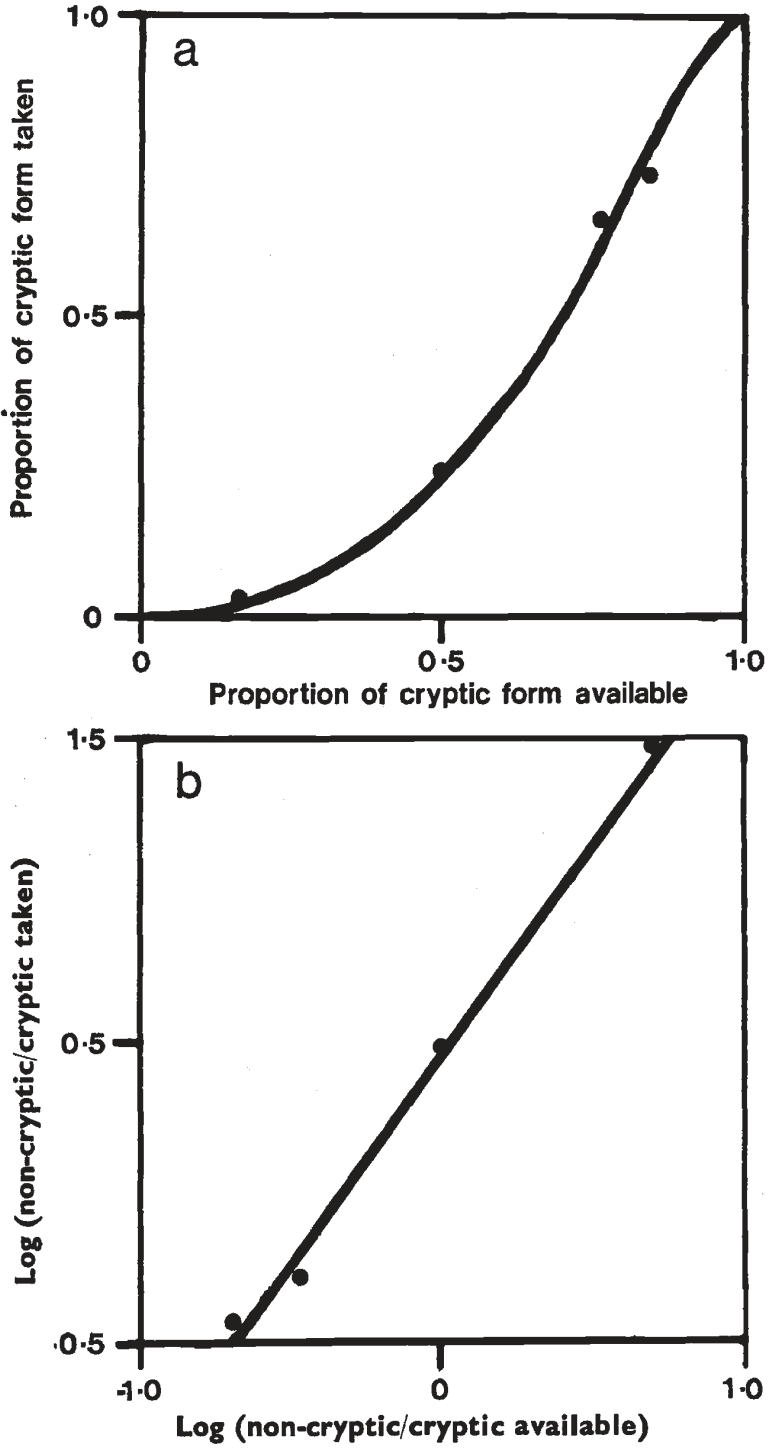


FIG. 1.—Fit to experimental data of Popham of lines estimated (a) by logit analysis and (b) by regression analysis.

3. The model is an adequate description of some experimental data which show apostatic selection.

4. The exactitude of fit of the model to the data suggests that there is not, as often thought, a high variance in the apostatic selection imposed by individual predators.

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ON THE POLYMORPHISM OF CYANOGENESIS IN *LOTUS* *CORNICULATUS* L.

III. SOME ASPECTS OF SELECTION

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1. INTRODUCTION

BUBAR AND LAWSON (1959) have shown that different varieties, strains and ecotypes of *Lotus corniculatus* L. exhibit differences in their ability to survive winter conditions in Canada. Bubar (1964, personal communication) has indicated that he has no evidence to suggest that acyanogenic plants are either more or less subject to winter injury than cyanogenic plants. This report contains the results of a formal investigation of (1) the problem of winter survival, (2) the production of seed by plants of different phenotype, and (3) the reanalysis of some data presented by Dawson (1941) and by Daday (1954).

2. SURVIVAL OF MATURE PLANTS

During the early summer of 1966 clones were established from 42 plants of *L. corniculatus*. In late summer the plants were arranged in the experimental field using a randomised block, spaced plant design. The original plants were grown from seed and represented the four possible phenotypes with respect to cyanogenic glucosides and β -glucosidase production and in most cases each clone was represented by 6 replicates. A grand total of 242 experimental plants were used and these were derived from 15 which