Frequency-dependent selection with background heterogeneity

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The response of predators to a choice of prey is influenced by prey frequency, density and visibility, and the type of background against which the predator is searching. These factors affect the likelihood that frequency-dependent predation will maintain polymorphisms. Experiments have been carried out in which human subjects searched a computer monitor screen for 'prey' objects (Ws and commas) against a background of randomly placed blocks of Ms and full stops (points). The frequency and density of the prey were varied, as well as their chance of occurring against the background element on which they are most cryptic. The display moved, so that only part could be seen at a time and the background frequency was also varied between trials. Under the conditions of most of the trials, rare objects were found more than proportionally (selection was anti-apostatic). Niche-choice by prey reduced this effect, as did a reduction in density. The relative visibility of the two prey objects changed with background frequency, as would be expected, but so did the frequency dependence. The data suggest that at one end of the range of background frequency the anti-apostatic effect changes to a pro-apostatic one which would maintain polymorphism. This result indicates that background variability may itself be an important factor in determining whether predators behave in such a way as to develop visible polymorphisms in prey species.

Keywords: density, distribution patterns, environmental heterogeneity, frequency-dependent selection, heterogeneity, selection.

Introduction

The response of predators to a choice of prey has been investigated from the point of view of optimization of predator effort (Greenwood, 1984), the handling of complex signals by the predator (e.g. Bond, 1983) and the ecogenetics of polymorphic prey species (Clarke, 1969; Murdoch & Oaten, 1975). It has been shown by a number of different groups that predators as diverse as birds and molluscs often take proportionally fewer of the rare forms of prey and more of the common forms than are available to them, thus exerting apostatic selection on the prey population (Clarke, 1962). This response may also be density-dependent. The response of predators to a choice of polymorphic prey (reviewed by Allen, 1988) is part of the more general question of how predators handle the problem of searching for prey with a variety of colour, pattern and degree of crypsis against complex backgrounds (reviewed by Endler, 1988). In birds, an apostatic (or pro-apostatic, Greenwood, 1984) response at relatively low densities has been shown to turn into an anti-apostatic response as the density increases (Cook & Miller, 1977; Horsley *et al.*, 1979; Allen & Anderson,

1984), so that rare types are taken proportionally more frequently, while in mammals the response has been demonstrated to be anti-apostatic (Greenwood *et al.*, 1984a, b). In addition to density, another factor which may affect the response is the degree of heterogeneity of the background from which the prey are taken. In land molluscs, for which apostatic selection has been suggested as the factor maintaining polymorphism, there is an association of polymorphic species with varied foliage backgrounds (Cain, 1977; Clarke *et al.*, 1978). It is not known to what extent this heterogeneity may itself create the conditions for polymorphism by allowing prey to associate with particular elements of their habitat, and to what extent it may affect the ability of the predators to make the appropriate choices (Cook, 1986a; Endler, 1988).

In any natural or experimental situation relative visibility, density and background heterogeneity interact, so that observations made with the intention of assessing their effects are difficult to control. For this reason, trials in which human subjects search for particular features on a computer monitor have some advantage over experiments in which non-human predators are used. A number of interesting results

have been obtained using this means (Gendron & Staddon, 1984; Tucker & Allen, 1988). The results presented here were designed to provide a manageable system in which effects of background heterogeneity and of background choice by prey could be assessed.

Materials and methods

The polymorphic snail *Littoraria pallescens* provided the model for which the computer program is an analogue. This species lives on mangrove tree foliage where patches of brightly illuminated green leaves are interspersed with dark areas of branch or shadow. Yellow morphs are less conspicuous than dark on leaves in the sun, while the darks are less conspicuous than yellow when in the shadow. When viewed from a few metres, the whole forms a structured but heterogeneous pattern on which the snails are visible but difficult to see (Cook, 1986b). In the computer program the background consists of randomly arranged rectangles consisting of two identical characters across by four down. The characters used were either Ms or full stops (points). On the monitor of the Apple II computers used, the images show up green against a black background, so that patches of bright green (Ms) alternate with darker patches of points. On this background, single units consisting either of Ws or commas represent the prey. The frequency of the background rectangles could be varied, as could the frequency and density of the prey units.

In some trials the prey units were distributed at random with respect to background, while in others they were not, thus representing niche choice. When there was niche choice a character falling within a patch of Ms had a higher than proportional chance of being a W, and if it fell within a patch of points it had a higher than proportional change of being a comma. This had the effect of causing larger divergences from the input frequency values than occur in the random placement trials. The actual frequency of presentation was then compared with the frequency recorded by the subjects.

The image on the screen scrolled for 160 s, as if a section of territory was being examined, only part of which could be seen at a time. Twenty-three rows of 40 columns could be seen at one time and a trial consisted of a display of 80 rows.

Human subjects faced the screen and were given a sheet of paper ruled into four columns. They were asked to identify any units they saw and record the number which appeared. In the first trials only two types were present but later two extra characters (Z and Q) were introduced, making up approximately 0.3 per cent of the units displayed, in order to add some

unexpected features. The program was then started and the number of units seen by the subject was recorded at the end of the run, together with the number displayed which was obtained from the computer. Almost all subjects were biology undergraduates or applicants who had come for interview on open days. They performed in one, or at most two, trials.

The experiments fall into five groups, all testing response to dimorphic prey.

1 Frequencies of commas, as opposed to Ws, of 0.2, 0.4, 0.6 and 0.8 were presented against nine background M frequencies from 0.1 to 0.9. The distribution of units was random and there were two replicates for each condition. The success of a morph at low frequencies is likely to be enhanced if it exerts background choice. In the *Littoraria* model system there is evidence that dark morphs tend to avoid exposure to the sun more than yellows, so that some background choice is exerted (Cook, 1986b). The following trial was therefore designed to investigate whether choice would change the relation of selectivity to presentation morph frequency.

2 Frequencies of commas of 0.1, 0.3, 0.5, 0.7 and 0.9 were displayed against eight background frequencies from 0.2 to 0.9, but background choice was introduced. There were three replicates for each condition.

3 In the above runs the density of display of units was 0.1, but it is known that the density has an effect on the likelihood of an apostatic response (Greenwood, 1984). A test was therefore conducted with densities of 0.1, 0.05 and 0.03 on a monomorphic background consisting entirely of Ms. There were three replicates of each condition.

4 The fourth experiment was run at the lower density of 0.05. Unit frequencies of 0.1, 0.3, 0.5, 0.7 and 0.9 were displayed against an M frequency of 0.5. There were two trials, with and without niche choice, and 10 replicates in each. Half the tests were run using undergraduates as subjects and half using applicants; it was therefore possible to extract another component from the error variance in the analysis.

5 The fifth group was designed to provide conditions favourable to an apostatic result, with a background frequency of 0.3 and niche choice. There were five presentation frequencies and two blocks of data each containing five replicates.

Analysis

For two morphs presented at frequencies A_1 and A_2, subjects detect e_1 and e_2, representing the frequencies eaten in a biological situation where there is predation. Subscript 1 refers to commas and 2 to Ws. A natural way to indicate selectivity is to calculate the logarithm

of the cross product ratio of fractions presented and eaten, i.e. $\log(e_1/e_2) - \log(A_1/A_2)$. A positive value indicated that relatively more commas have been detected than would be expected on the basis of proportionality, so that if that type were a morph in a prey species it would be at a disadvantage. A negative value indicates that relatively few have been detected, corresponding to a prey advantage. Selectivity has been calculated in this way for every presentation.

The selectivity measures both the basic difference in detectability between the two morphs and any frequency-dependent difference which may be operating under particular conditions. Several methods have been developed to separate these, which depend on assumptions made about how frequency affects response (Gendron, 1987). Greenwood & Elton (1979) distinguish two components by writing $\log(e_1/e_2) = b \ \log(VA_1/A_2)$. The coefficient b is a measure of the frequency-dependent difference in detectability between the morphs, and V measures the frequency-independent difference. Where a range of values of A_1 has been used, these parameters may be estimated from the regression of frequency detected on frequency presented, and this has been done for sets of data from each trial. If b is greater than 1 the prey morph is at an advantage when at low frequency and a disadvantage at high (apostatic selection); if it is less than 1 the reverse is true and there is anti-apostatic selection. When V is greater than 1 the form is more easily detected, and when less than 1 less easily detected than its alternative, independently of frequency. In this analysis both b and V refer to commas.

Results

1 *Random distribution, high density.* The variation in selectivity with frequency of presentation and background frequency is shown in Table 1. Both components have a significant effect, while there is no evidence of interaction. The effect of background is what would be expected; commas are relatively protected when the background consists mostly of points and become progressively easier to detect as the frequency of Ms increases. At low frequencies of presentation commas are equally as detectable as Ws, but become relatively less so as their frequency increases.

2 *Background choice, high density.* The analysis of variance is shown in Table 2. Again, the variation is significant with respect to both presentation frequency and background frequency, but there is no interaction. The relation of selectivity to presentation frequency is often more positive and commas are more easy to detect.

3 *Effect of density.* Subjects were presented with a background consisting entirely of Ms on which Os and Bs appeared at frequencies of 0.1, 0.3, 0.5, 0.7 or 0.9. The density of display was 0.1, 0.05 or 0.03. The results are shown in Table 3. There is no detectable effect of density over the densities used, but the effect of presentation frequency is very significant. Selectivity declines from positive values at low frequency to negative ones at high, so that the effect is anti-apostatic. Previous studies have shown that anti-apostatic behaviour is associated with a relatively high density, so that despite the lack of significance in the test the decision was made to run future tests at densities of 0.05. This

Table 1 Random distribution of prey objects at density of 0.1. Analysis of variance for selectivity values at different frequencies of prey and background is given at top. Mean selectivity for each morph frequency and background frequency is shown below along with the estimates of b and V at each background frequency

Component	d.f.			Mean square			F	P
Prey morph frequency	3			0.486			3.71	<0.05
Background elements	8			1.330			10.15	<0.001
Interaction	24			0.177			1.35	ns
Error	36			0.130				
Morph frequency	0.2	0.4		0.6		0.8		
Mean	0.059	−0.085		−0.120		−0.339		
Background	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
Mean	−0.407	−0.668	−0.470	−0.413	−0.240	0.009	0.352	0.185	0.528
b	0.91	1.05	1.03	1.03	0.79	1.09	0.62	0.54	0.71
V	0.64	0.54	0.65	0.67	0.74	1.01	1.78	1.41	2.10

Table 2 Selectivity with prey exhibiting niche choice at density of 0.1. Analysis of variance for selectivity values at different frequencies of prey and background is given at top. Mean selectivity at each morph frequency and background frequency is shown below, along with estimates of b and V at each background frequency

Component	d.f.			Mean square			F	P
Prey morph frequency	4			0.316			3.69	<0.01
Background elements	7			0.424			4.94	<0.001
Interaction	28			0.097			1.13	ns
Error	80			0.085				

Morph frequency	0.1	0.3	0.5	0.7	0.9			
Mean	0.210	0.290	0.104	0.085	−0.005			

Background	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
Mean	−0.109	−0.076	0.013	0.221	0.244	0.350	0.172	0.267
b	1.11	1.08	0.95	0.98	0.89	0.86	0.93	0.89
V	0.66	0.80	0.82	1.01	1.05	1.19	0.98	1.08

Table 3 Effect on selectivity of varying density on a monomorphic background. Analysis of variance for selectivity at different morph frequencies and densities is given at top. Mean selectivity at each morph frequency and density is shown below, along with the estimates of b and V at each density

Component	d.f.	Mean square	F	P
Prey morph frequency	4	0.518	9.34	<0.001
Density	2	0.023	0.41	ns
Interaction	8	0.016	0.29	ns
Error	30	0.056		

Morph frequency	0.1	0.3	0.5	0.7	0.9
Mean	0.235	0.067	0.014	−0.268	−0.340

Density	0.1		0.03		0.05
Mean	−0.067		−0.093		−0.015
b	0.79		0.91		0.89
V	0.94		0.88		0.81

Table 4 Comparison of random distribution and niche choice at density of 0.05 and background frequency of 0.5. Analysis of variance for selectivity at different morph frequencies and with the two distribution patterns is given above. Mean selectivity at each morph frequency and distribution pattern are shown below, along with the estimates of b and V for the two distribution patterns

Component	d.f.	Mean square	F	P
Prey morph frequency	4	1.104	6.02	<0.001
Distribution pattern	1	0.768	4.19	<0.05
Frequency × distribution	4	0.263	1.43	ns
Other interactions	10	0.201	1.10	ns
Error	180	0.183		

Morph frequency	0.1	0.3	0.5	0.7	0.9
Mean	0.032	0.260	−0.066	−0.111	−0.160

Distribution pattern	Random	Niche choice
Mean	−0.071	0.053
b	0.92	0.93
V	0.93	1.05

figure is a compromise between providing a low density and ensuring sufficient sightings during an acceptable searching period.

4   Comparison of distribution patterns. The results are shown in Table 4. The effect of presentation frequency is again highly significant and the difference between results, where there is random distribution as opposed to background choice, is also significant. No other component was significant. As suggested by the first two trials, the result of background choice has been to make commas more visible on average than they are when the prey units are randomly distributed.

5   Niche choice with a background frequency of 0.3. The results of this test are shown in Table 5. The difference between presentation frequencies is again significant. The difference between blocks is not significant

but is relatively large. Selectivity declines from a low frequency of presentation up to 0.7, but at 0.9 it is again positive.

Selectivity decreasing from positive values at low frequencies of presentation to negative ones at high indicates an anti-apostatic effect. This is the most common result in the tests. Measured in this way, however, the frequency-dependent and frequency-independent elements of the selection are confounded. Where regression of detection frequency on presentation frequency can be estimated they can be separated using the Elton method. The parameters b and V have been estimated for all the separate datasets making up the groups of tests. These have been entered on the

Table 5 Selectivity with prey exhibiting niche choice at a background frequency of 0.3 and a density of 0.05. Analysis of variance for selectivity at different morph frequencies is given at top. Mean selectivity at each morph frequency is shown below, along with estimates of b and V

Component	d.f.	Mean square	F	P
Prey morph frequency	4	0.651	3.20	<0.05
Blocks	1	0.634	3.11	ns
Interaction	4	0.229	1.12	ns
Error	40	0.203		

Morph frequency	0.1	0.3	0.5	0.7	0.9
Mean	0.820	0.127	−0.352	−0.282	0.209
b	0.99				
V	0.96				

Fig. 2 Relation of frequency-independent coefficient V to M presentation frequency. Each point is an estimate from a regression analysis. ($\bigcirc$) Random placement trials; ($\square$) niche choice trials. Vertical lines represent standard errors of estimates. There is no frequency-independent selection when $V = 1$. The curved line is the regression of log V on M presentation frequency.

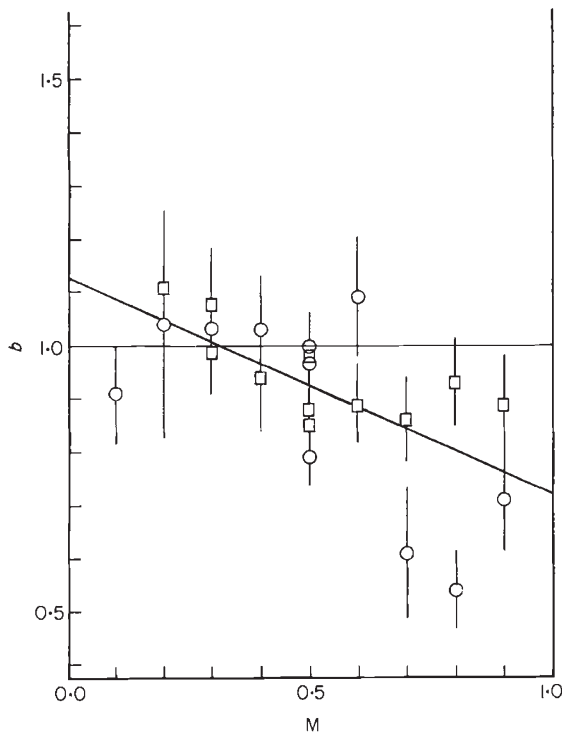**Fig. 1** Relation of frequency-dependent coefficient b to M presentation frequency. Each point is an estimate from a regression analysis. ($\bigcirc$) Random replacement trials; ($\square$) niche choice trials. Vertical lines represent standard errors of estimates. There is no frequency-dependent selection when $b = 1$; the regression line for all data is shown.

respective tables and are plotted on background frequency. Figure 1 shows the relation of the frequency-dependent coefficient b to background frequency and Fig. 2 shows the independent coefficient V. If we consider all values as having equal weight, the regression of b on background frequency is significant ($t = 3.57$,
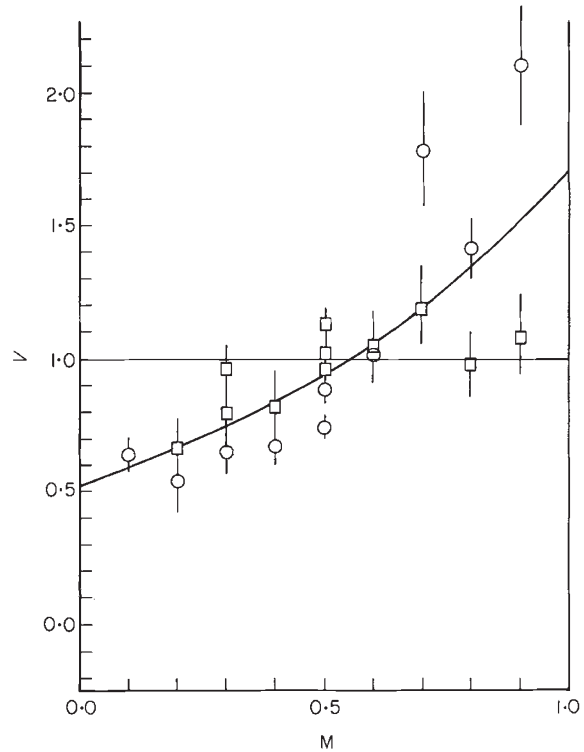
$P < 0.01$), as is the regression of log V ($t = 6.21$, $P < 0.001$). The two parameters have a significant negative association (using Kendall's Tau, $t = 3.36$, $P < 0.01$). The regression suggests that the apostasis parameter b has a value of 1 at a background frequency of 0.30, while V is 1 at a background frequency of 0.56.

Discussion

The results indicate that human subjects tend to find objects in a non-proportional manner when presented with pairs of alternative characters against a background of other characters, each of which resembles one of them. It may be objected to that the characters chosen are familiar, and have connotations different from the prey used in animal searching experiments. It might have been better, for example, to have used a Cyrillic or Thai character set; also the reward for success is different. Nevertheless, the confusion in the response occasioned by varying frequency or background is likely to be common to all such choosing

tasks and not just to searching for prey. The procedure used allowed conditions to be manipulated and, in particular, permitted the field of view to move, as if a predator were scanning a range of territory. The high error mean squares in the analyses of the tests show that a good deal of the variance is unaccounted for but this is also common in tests in which animals choose prey (for references, see Allen, 1988).

Where the background frequency was varied, the mean selectivity changed from negative to positive values with an increase in background M frequency (Tables 1 and 2). This result is in the direction expected; commas were relatively more easy to detect than Ws against a high frequency of Ms than a low one. It does, nevertheless, establish that in the experiments the background influenced the ability of the subjects to discriminate.

A change from random distribution to niche choice appears to render commas relatively more visible. This can be seen by comparing Table 1 with Table 2 and is confirmed in Table 4. A change in distribution of the prey has affected the response of the predators, although it has not noticeably changed the frequency-dependent element.

The separation of the frequency-dependent component, b, from the independent component, V, reveals that in most trials selection is anti-apostatic. This is undoubtedly in part because of the heightened attention given to novel stimuli. In the last three runs a few Zs and Qs were added to increase the range of features present. In all, 11,799 Ws and 12,556 commas were displayed in the tests in Tables 4 and 5, and 85 Z plus Qs. Eighty-six per cent of the latter were detected, compared with 48 per cent Ws and 51 per cent commas. Under the conditions of the experiments human subjects are more likely to show evidence of attention to rare features than of any kind of optimum search routine, which leads to a greater success in finding common ones. Figure 1 shows, however, that the strength of the frequency-dependent effect is related to background frequency, and it suggests that an anti-apostatic response is converted into an apostatic one at background M frequencies lower than 0.3.

Cook (1986a) argued that background heterogeneity is not necessary for frequency-dependent selection, so that the association of molluscan polymorphisms with background heterogeneity (Clarke et al., 1978) may be because the heterogeneity allows niche choice on the part of the prey, rather than apostatic selection on the part of predators. The alternative would be that it is only when the sensory input received by the predators is confused by a varied background that conditions favour the apostatic response. In these experiments it is shown that frequency-dependent

response may occur against a monomorphic background (Table 3. Two of the b values are significantly less than 1) and that niche-choice may influence the predators' behaviour (Table 4), although neither of the effects demonstrated would generate polymorphism. The results illustrated in Fig. 1, however, do indicate that the right combination of elements in the background may result in apostatic selection although other mixtures will not do so. This favours the contention that an effect of heterogeneity on predator response, rather than on prey distribution, is important. Overall, the results show how volatile the response is and that all these effects may be involved in establishing whether or not polymorphism will be generated in a given ecological situation.

Acknowledgements

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