distribution of the enzyme activity within the broad band should initially be skewed towards the F form and tend to the S form as the proportion of S isozyme is increased. The same test can be made genetically using tetraploid stocks carrying different doses of the *Gdh* alleles and thus avoid having to dissociate and reassociate the enzyme *in vitro*.

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SELECTION BEHAVIOUR OF WILD BLACKBIRDS AT HIGH PREY DENSITIES

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Summary

In experiments with wild blackbirds eating artificial pastry baits of two colours presented at high density. it has been argued elsewhere that selection was directional. The experiments have been repeated with a slightly different experimental design and the results indicate apostatic selection. Some indications of changes in selection behaviour by the blackbirds, both within and between visits, are also mentioned.

1. Introduction

As a result of the development of a " specific searching image " (Tinbergen, 1960) predators may preferentially take the more common varieties of a

variable prey species; such selection is apostatic (Clarke, 1962). Using dyed pastry baits Allen and Clarke (1968) demonstrated that ground feeding passerines tend to hunt in this way and since they are important predators of many polymorphic prey species they could maintain visual genetic polymorphisms. In a later paper Allen (1972) reported contrasting effects of prey density on the selection behaviour of wild blackbirds (*Turdus merula* L.). He analysed two series of experiments using brown and green pastry baits of similar hue and brightness (*The Munsell Book of Color*, 1966): in one the baits were presented at low density (200 baits per 100 m square) and in the other they were presented at high density (300 baits per 19 cm diameter metal sieve). In both experiments the prey population of cylindrical baits (0·7 cm long × 0·7 cm diameter) contained 90 per cent brown and 10 per cent green with replicates of 10 per cent brown and 90 per cent green. In

TABLE 1

A hypothetical example of a specific searching image leading to apparent directional selection in adjacent populations with predators taking 30, 20 and 10 prey in successive time intervals during an interrupted feeding period. Numbers denote prey taken. Expected calculated from 9 : 1 ratio

Time period	Sieve 1 (270 brown: 30 green)			Sieve 2 (30 brown: 270 green)		
	Bird	Brown	Green	Bird	Brown	Green
1	A	28	2	B	2	28
2	A	19	1			
2	B	10	10			
3	B	7	3	A	8	2
Total baits taken		64	16		10	30
Expected		72	8		4	36

the low-density experiments blackbirds preferentially chose the more common morph and in the high-density experiments they chose the less common morph. It thus appeared that selection by wild blackbirds was directional (Allen uses the term stabilising) when baits were at high density and apostatic at lower density.

In the high-density experiments of Allen two sieves containing the baits at different colour frequencies were placed 1 m apart on a lawn at the Department of Zoology, University of Edinburgh. We have noticed that when blackbirds are feeding from artificial populations they occasionally move around, even in the presence of ample food supplies. If blackbirds moved between sieves while feeding, the development of a specific searching image could, under certain conditions, lead to apparent directional selection. For instance if the pair of blackbirds that Allen reports moved between sieves during feeding then selections of the rarer morph from one sieve may be a result of a specific searching image formed for the common morph at the adjacent sieve. Obviously the particular results obtained would depend on various factors such as the strength and duration of the specific searching image or the frequency of movement between sieves. A hypothetical example in table 1 shows how apparent directional selection could occur. Although both birds develop a searching image which can change during the time of feeding, nevertheless apostatic selection is not evident from the final results. Moreover, if the blackbirds in Allen's experiment did always feed from the sieve in the same position then the fact that the relative position o

the two sieves was frequently altered could lead to a situation similar to that suggested above.

2. Results and discusson

We have repeated Allen's high-density experiments with wild blackbird predators on lawns at Failsworth, Manchester during July 1973 with sieves placed about 2000 m apart and the results in table 2 were obtained. These results are quite different from those reported by Allen and demonstrate

Table 2

Totals of baits taken each day during the high-density experiment. Expected calculated from 9 : 1 ratio —population replenished to original for each day

	30 brown: 270 green		270 brown: 30 green	
Day	Brown	Green	Brown	Green
1	4	8	24	2
2	12	102	38	3
3	12	131	59	2
4	11	136	109	7
5	13	111	124	5
6	8	158	95	6
7	9	151	55	3
8	7	86	64	2
9	8	96	71	3
10	13	141	92	3
11	10	132	101	4
12	5	127	76	5
13	6	154		
14	13	168		
15	6	162		
16	12	128		
17	8	152		
Total	157	2143	908	45
Expected	230	2070	857·7	95·3

very obvious selection by the birds for the bait at higher frequency at both sites. The results are not amenable to analysis by chi-squared testing owing to the differences in the proportions taken between days. Nevertheless, in only three of the 29 presentations did blackbirds take higher than the presented frequency of the less common morph and these were during the first 6 days of the high green frequency experiment. In both cases the number of baits taken tended to increase and the frequency of the less common morph taken tended to decrease on successive days. For the case of high green frequency, we have calculated β (Manly, 1973), the probability that the next individual selected would be brown if the blackbirds had a choice from an equal number of baits in the two colour classes. Product moment correlation (r) on the data (normalised after ranking) show that β is negatively related to the number of the visit and to the number of baits taken (respectively, $r = -0{\cdot}62$ and $r = -0{\cdot}70$, in both cases $P < 0{\cdot}01$). The number of baits taken is still negatively correlated with β after the effect of time has been removed by partial correlation ($r = -0{\cdot}56$, $P < 0{\cdot}05$). This indicates that the strength of the searching image probably increases during feeding and that as more baits are taken on any particular day it is less likely that they

will be brown. The negative correlation between the number of the day and β remains significant only at the 10 per cent level ($r = -0{\cdot}41$) after removing the influence of the number of baits taken using partial correlation. This indicates an increasing intensity of the searching image on successive visits. Although the data show reciprocal patterns in the trials with high brown frequency, none of the relevant correlations is significant at the 5 per cent level.

It is therefore unlikely that the results at the site with high green frequency are a consequence of the blackbirds having an initial preference for green baits. However, the results at the site with high brown frequency could be interpreted in terms of a preference for brown baits maintained through the experiment. It should be pointed out that results in experiments of this type may be influenced by changes in availability of prey outside the confines of the experiment. Any conclusions drawn must therefore be tentative.

3. Conclusions

We consider that these experiments indicate selection behaviour by blackbirds that would tend to maintain a rare colour morph in a prey population at extremely high density.

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THE DEFINITION OF THE TERM DISRUPTIVE SELECTION

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The term " disruptive selection " was introduced by Mather (1953). It is selection applied to the phenotypes of a variable population which " may favour both extremes simultaneously, though not necessarily to the same extent, at the expense of the average " (*loc. cit.*, p. 73). As a result it will convert an originally unimodal normal distribution into a bimodal