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APOSTATIC SELECTION: THE RESPONSES OF
WILD PASSERINES TO ARTIFICIAL POLYMORPHIC PREY

by

John Ashdown Allen



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ABSTRACT

The maintenance of non-mimetic colour polymorphism has yet to be satisfactorily explained. Apostatic selection is one possible answer: sight-dependent predators may tend to form 'searching images' for common morphs and concentrate on these varieties in preference to rarer ones. (Chapter I).

Some evidence for apostatic selection exists, but it is mostly indirect and incomplete. (Chapter II).

The hypothesis was tested by experiments with wild passerine birds in their normal surroundings. The prey were lard-and-flour 'baits' which were usually green or brown and cylindrical (0.7cm long x 0.7cm diameter). Data were obtained by direct or indirect observation of 'populations' containing the colours in known proportions. Eaten baits were replaced frequently to ensure that the ratios were kept constant. Five sets of experiments were carried out. (Chapter III).

In one set (Chapter IV) baits were at maximum density. When unequal numbers of greens and browns were presented there was a significant overall tendency for the rarer forms to be removed. Individual blackbirds Turdus merula tended to concentrate on one colour alone within visits. Presentation of greens and browns in equal numbers gave no evidence that the colours differed in taste. Further experiments with small green and brown baits and small red and yellow baits confirmed that rare forms are preferred at maximum density.

In the remaining sets of experiments baits were at a density of two per square metre. Populations of randomly distributed greens and browns were presented on grass or soil backgrounds.

A second set of experiments (Chapter V) revealed that birds can become conditioned to searching for either green or brown baits. Wild birds were fed with one colour alone and were then given populations with both colours in equal proportions. In all eight experiments the familiar colour was strongly preferred. In three cases the preferences were reversed by a further training period on the 'unfamiliar' colour.

A third set (Chapter VI) showed that passerines, on average, tend to take more of the common variety than expected on the basis of constant selection. In each experiment populations were presented either with greens nine times as common as browns followed by populations with browns nine times as common as greens, or in the reverse order. The initial study revealed heterogeneity within the data and repeat experiments were therefore carried out. The data from the fourteen experiments were consistent. In thirteen cases the common colour was preferred overall, despite different environmental conditions.

A fourth set investigated the behaviour of individual blackbirds and songthrushes Turdus philomelos. One experiment (Chapter VII) showed that the three birds involved preferred browns. In two cases these preferences were very strong and the birds started to eat greens in quantity only when browns were very rare. This behaviour was preceded by an increase in the tendency to 'imprint-peck'. The three birds appeared to differ markedly

in their responses. Two further experiments (Chapter VIII) with a majority of 'new' birds confirmed the above findings and also provided evidence of searching images. At the end of the third experiment populations of green, browns and khakis were offered. The khakis were initially overlooked.

In a fifth set (Chapter IX) greens, browns and various shades of khaki were used. Two series of experiments tested the specificity of conditioning. Birds were familiarized with one colour and were then offered populations with the 'familiar' bait and a visually similar colour in equal proportions. They were then trained on the 'unfamiliar' colour and given a choice as before. The results showed that birds can become conditioned to a particular colour; this conditioning can be very specific, but reversible. In two further experiments an attempt was made to see whether predators can promote polymorphism. Blackbirds and songthrushes were offered populations containing nine morphs ranging from green to brown and in proportions that fitted the normal distribution. These proportions were altered regularly to accord with the frequencies that remained after a fixed percentage of baits had been eaten. One experiment showed that the brownest baits were preferred. The second experiment was preceded by a period of familiarization with the commonest khaki morph and showed an increase in the variance of the population. The distribution became bimodal. This disruptive effect was probably a result of the training, natural brown preferences, and the heterogeneity of behaviour of the birds. Searching images can therefore be very specific and under certain conditions predators may be capable of causing polymorphism in prey species.

The experimental design is considered to resemble a natural situation. It is concluded that the results support the hypothesis of apostatic selection. The findings have implications for the conditions under which apostatic selection is likely to act and point the way to future research. It is suggested that a number of different types of apostatic polymorphism exist. (Chapter X).

PREFACE

My aim in this work has been to test a hypothesis. It has been suggested that variability within a population of a palatable prey species can be maintained by 'apostatic selection' by predators, the meaning of which will become clear later. This possibility has been investigated by presenting populations of artificial prey to wild passerine birds in their normal surroundings. The exercise is therefore situated in the area of zoology where animal behaviour and population genetics overlap. We are concerned with the behaviour of predators, and more important, with its effect on variability in the prey population.

The thesis is organised into ten Chapters. The first is introductory and provides the background to the problem. Existing evidence for apostatic selection is reviewed in the second Chapter. A description of the general experimental approach is given in the third and the experiments themselves are discussed in the following seven Chapters. Bulky data are tabulated in appendices at the ends of the relevant Chapters. The final Chapter focuses on the main conclusions and points out possible lines of future research.

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CHAPTER I GENERAL INTRODUCTION

CHAPTER 1 GENERAL INTRODUCTION

1. COLOUR POLYMORPHISM AND ITS MAINTENANCE

Individuals of some species can be classified into a number of distinct forms living in the same population at the same time. When the rarest 'morph' is present at a frequency too high to be accounted for by mutation, this variation is defined as 'polymorphism' (Ford 1940). It usually has a genetic basis and may be detected at different positions along a biochemical pathway; from close to the action of the gene, as in enzyme polymorphism, to actually visible alterations of morphological characters. At this end of the system, the colour or colour-patterning of the organism may be involved.

Some colour polymorphisms (as perhaps in Biston betularia L., Kettlewell 1958) may only be transient, with one morph gradually replacing another. Others appear to be relatively more stable. This latter, balanced, type poses the more interesting evolutionary problems, in particular with regard to how it is maintained.

The possible mechanisms capable of maintaining genetic polymorphism have been examined theoretically by a number of authors (e.g. Dempster 1955, Sheppard 1958, Williamson 1958, Maynard Smith 1962, Ford 1965). In practice, however, the relevant selective forces have rarely been identified. One possible exception concerns polymorphic mimicry in certain tropical Lepidoptera (e.g. see Clarke and Sheppard 1960 for Papilio dardanus Brown, Ford 1953 for Hypolimnas misippus L.). In these, some or all of the morphs mimic other more distasteful species. A mimetic morph will be favoured so long as its frequency relative to the model remains low. Once the frequency of the morph increases its advantage starts to diminish. A definite disadvantage will occur when it is so common that its conspicuous coloration

becomes associated with palatability rather than the opposite.

Other morphs may therefore be at a relative advantage and a balanced polymorphism can result.

However, there are many examples of colour-polymorphism where mimicry is not clearly involved. They are to be found throughout the Animal Kingdom. Because of lack of space it is impossible to give a complete, or even representative, list and no comprehensive review exists. It is hoped that the following examples give some idea of the range of species involved:

Metridium senile (Coelenterata, Anthozoa), Fox and Pantin (1961).

Pomatoceros triqueter (Annelida, Polychaeta), Føyn and Gjøn (1954).

Cepaea spp. (Mollusca, Gastropoda), various authors.

Sphaeroma rugicauda (Crustacea, Isopoda), West (1964).

Armadillium nasutum (Crustacea, Isopoda), Adamkewicz (1969).

Philaenus spp. (Arthropoda, Hemiptera), Halkka and Lallukka (1969).

Homorocoryphus nitidulus (Arthropoda, Orthoptera), Owen (1965c).

Ophiocemina nigra (Echinodermata, Ophiuroidea), Fontaine (1962).

Xiphophorus maculatus (Chordata, Pisces), Gordon and Gordon (1957).

Eleutherodactylus spp. (Chordata, Amphibia), Goin (1950).

Malaconotus spp. (Chordata, Aves), Hall et al. (1966).

Colour-polymorphic species inhabit a diverse range of environments, both marine and terrestrial, and their distribution is world-wide. The degree of polymorphism varies from species with two morphs (e.g. the larvae of the moth, Geometra papilionaria L.) to species possessing almost infinite variation (e.g. the butterfly clams, Donax spp.). Within species, there are often very distinct visible differences between the morphs. Indeed such variation has in the past created taxonomic confusion. Until recently, the different

phases of the bush-shrikes (Malaconotus) were considered as separate species, simply because they looked so different (Hall et al. 1966). Similarly, the 170 African species of the land-snail Limicolaria have now been reduced to 17 (Crowley and Pain 1970).

How, then, are these non-mimetic polymorphisms maintained? Faced with a lack of evidence for one mechanism or another, many workers have assumed that heterozygous advantage is involved. Documented examples of such views pertain to Cepaea spp. (Cain and Sheppard 1954a, Ford 1964); Malaconotus spp. (Hall et al. 1966) and the platyfish Xiphophorus maculatus Günther (Gordon and Gordon 1957). It is true that there is definite evidence that heterosis can maintain a polymorphism (for instance in the classic case of sickle-cell anaemia, Allison 1956), but its ubiquity as a mechanism has yet to be demonstrated. With regard to colour polymorphisms, this lack of positive evidence may, admittedly, often be due to the difficulties of distinguishing between homozygotes and heterozygotes in the wild. This is especially true for organisms, like Cepaea, where there is still no satisfactory method of distinguishing the dominant genotypes.

Heterosis is by no means the only mechanism capable of maintaining a polymorphism. Other possibilities have been discussed in detail by Williamson (1958) and other authors previously mentioned (p. 18). More specifically, Clarke (1962a) has examined these mechanisms with regard to colour-variation, particularly in Cepaea. He concluded that the colour and banding polymorphisms of these species are probably maintained by selective predation, in the absence of mimicry. This thesis focuses on such a mechanism.

2. SELECTION BY PREDATORS

(a) General

Before considering this possibility in detail, it is instructive to examine some more general aspects of the relationships between predators and polymorphic prey. We can best discuss these features with reference to the well-known land snails Cepaea nemoralis L. and C. hortensis Müll. These species are sympatric over a large part of the British Isles and inhabit both grasslands and woodlands. They are highly polymorphic for the colour and banding patterns of their shells, and the genetics of these characters have been worked out (Cain, King and Sheppard 1960; Cook 1967; Cain, Sheppard and King 1968).

In Britain, the main predators of Cepaea are the songthrush Turdus philomelos Hart., various rodents, and rabbits. The most relevant to our problem are the former, since they hunt almost exclusively by sight, whilst small mammals are more dependent on olfactory cues. In addition, the thrush definitely possesses colour vision (van Eck 1939), whilst rodents and rabbits discriminate only in terms of black and white (Walls 1942). Hence, mammalian predators selectively predate those morphs of Cepaea that contrast in tone with the background (Cain 1953). It follows that the colour of a morph taken by a rodent is not necessarily the same as that attacked by a thrush under the same conditions.

Selection of palatable animals contrasting with their background is now well-accepted (see Cott 1940) despite the assertions of earlier workers like Selous (1908) and Pearl (1911). Experiments on the moth, Biston betularia, are classics in proving that conspicuous palatable prey are picked out in preference to those harmonizing with

the background (Kettlewell 1955). Balanced polymorphic species are also subject to strong visual selection. The colours of C. nemoralis morphs often correspond with the coloration of the background, due to selection by thrushes (Sheppard 1951). A similar effect occurs in C. hortensis, though the correlation with the background may be due to a different genetic response by the snail; for example, the commonest morph found on leaf litter in beech-woods is not unbanded brown as in C. nemoralis, but five-banded yellow, with all the bands fused (Clarke 1960). Colour-polymorphisms in other species are also subject to changes in morph-frequency, probably due to visual selection (e.g. in water-snakes, Natrix spp., Camin and Ehrlich 1958; in Limicolaria martensiana, Owen 1965a).

If polymorphism in Cepaea is maintained by non-visual effects, then years of selection by predators should have produced the evolution of a uniform shell-colour appropriate to the colour and texture of the environment. Yet the morphs are still distinct in appearance, and have been for at least thousands of years. Sub-fossil Cepaea shells still reveal some of the discontinuity of the variation they possessed when alive, since the bands remain discernable (Diver 1929). Similar evidence for the durability of colour-pattern polymorphisms has been found in other gastropods, for example, Limicolaria (Owen 1966b) and Velacumantus (Ewers 1966). If sufficient specimens of true fossil polymorphic gastropods exist, the banding variation might still be visible. Distinct patterns can be retained on specimens as ancient as Devonian trilobites (Esker 1968) and even older Cephalopods and Brachiopods (Foerste 1930).

It is therefore tempting to suggest that some type of predator-controlled mechanism is maintaining Cepaea and other non-mimetic polymorphisms. We must now consider what form it is likely to take.

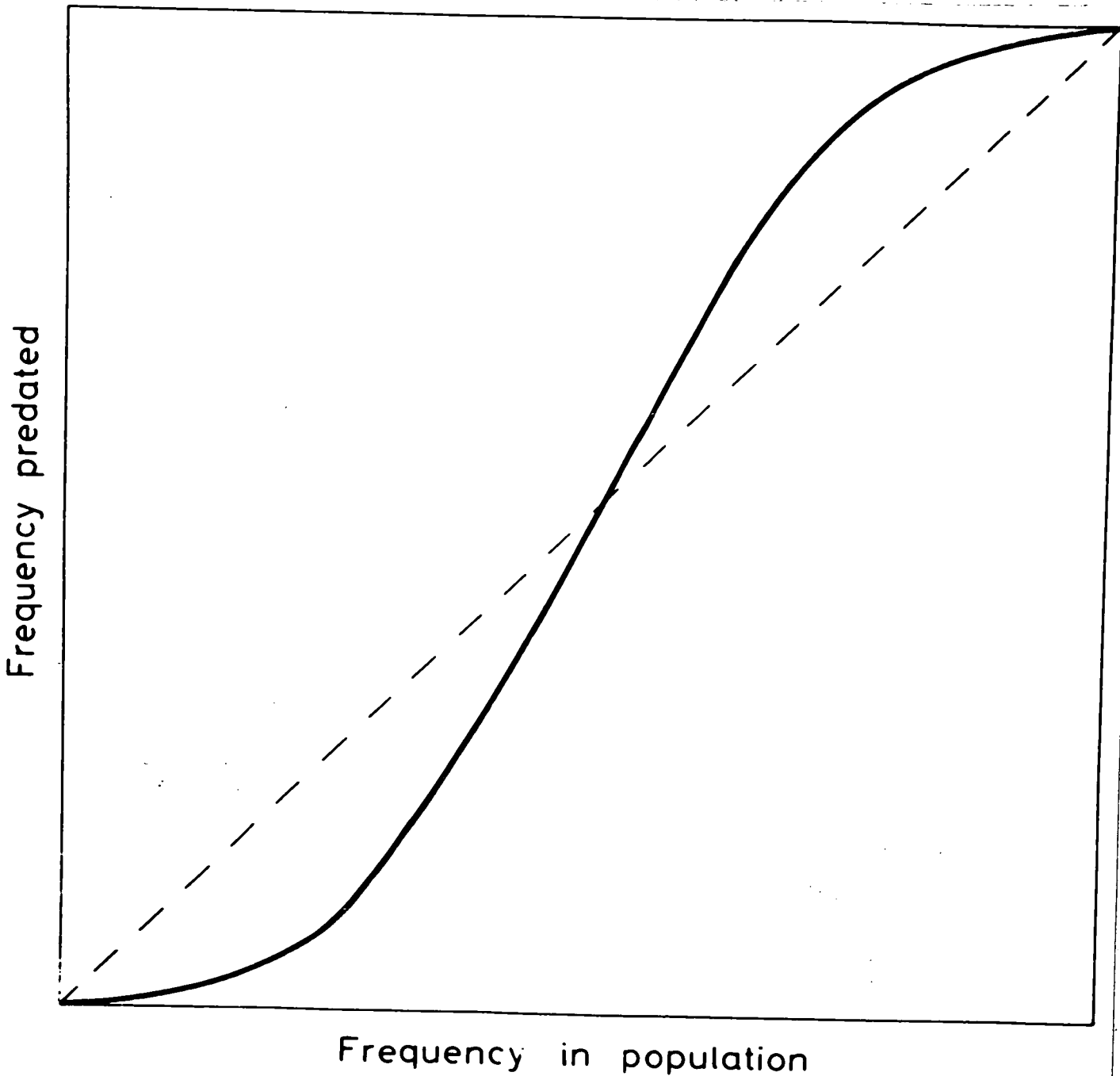


Figure 1

The frequency of a morph in a population plotted against the frequency predated. The broken line shows the expected relationship if predation is random. A hypothetical example of apostatic selection is given by the continuous line; the morph is over-predated at high frequencies and under-predated when rare. Note that this simple example does not involve additional frequency-independent selection; the sigmoid curve is symmetrical about the discontinuous line.

Cain et al. (1960) stated that some morphs of Copasa seem to resemble components of their habitat and are therefore kept distinct by predators. Owen (1966a) has presented a similar case for a polymorphic East African species of grasshopper, Homocoryphus nitidulus. It was realised by Cain et al., however, that selection on this basis could not maintain a polymorphism, since it would be frequency-independent. In addition, it has been argued that some morphs (e.g. bright pinks of Copasa and pallids of Limicolaria martensiana) are conspicuous against all backgrounds (Clarke 1962a, 1969; Owen 1963a).

(b) Apostatic selection

It is now opportune to present a method of selection by predators that may be capable of maintaining polymorphisms in the absence of mimicry. Theoretically, the system is simple. It relies on the premise that predators preferentially search for, and eat, the most common morphs of a polymorphic species. Under such conditions the rarer forms, even if relatively conspicuous, should be protected from predation and hence be maintained in the population (see Fig. 1).

The mechanism is frequency-dependant since the fitness of the genotype (and therefore the gene) is inversely related to its frequency. That this type of selection can maintain a polymorphism has been demonstrated many times (Wright 1948, Li 1962, Haldane and Jayakar 1963, Clarke and O'Donald 1964). In this dissertation, the term 'apostatic selection' (Clarke 1962a) will be used for frequency-dependant selection that maintains a colour-pattern polymorphism, since such a mechanism promotes 'apostasy'. That is, it favours those morphs, or 'apostates' that are visually different from the majority (Clarke 1962a)¹.

¹'Apostasis' (Cooke 1965) is synonymous with 'apostatic selection'. 'Apostatic polymorphism' (Clarke 1962a) is polymorphism maintained by apostatic selection.

Historically, the hypothesis was originally suggested by the eminent naturalist Poulton (1884) to explain dimorphism in the caterpillars of the Large Emerald Moth, Geometra papilionaria L. The idea was first applied in relation to Cepaea by Cain and Shoppard (1954a), whilst Maldane (1955) also suggested that birds have to learn that particular Cepaea visual patterns are signs of edibility and hence maintain the polymorphism. More recently, Clarke (1962a, 1962b, 1969), has taken up the cause that apostatic selection is maintaining the shell polymorphism of Cepaea. Since then, the hypothesis has been invoked to explain many other cases of colour-pattern polymorphisms (e.g. Limicolaria, Owen 1963a, 1963b, 1965a; Malaconotus, Owen 1967; Philaenus, Owen and Weigert 1962, Halkka and Lallukka 1969; Nerita, Safriel 1969; Hyperolius, Schiøtz 1971). Payne (1967) has advanced the hypothesis that polymorphism in cuckoos and raptors minimises the chances of recognition by host and prey species. If this were true, apostatic selection would be acting 'in offence'. Rarer morphs would be at an advantage over commoner forms because they would tend to parasitise or destroy disproportionately more victims.

Moment (1962) pointed out that predators may be responsible for the nearly infinite variation found in, for instance, some brittlestars (Ophiuroidea) and Butterfly Clams (Donax spp.). In other words the population as a whole benefits because there is no repeatable visual cue for a predator to learn. Moment called this type of selection 'reflexive' because "the frequency of any one type is determined by a feedback relationship with all the other types". However, it is difficult to speculate how such a polymorphism could evolve (apart from invoking group selection, Wynne-Edwards 1962), other than by frequency-dependent selection. This fact seems to have

been realised by Li (1962) when reinforcing Moment's hypothesis with mathematical evidence.

Colour-pattern polymorphisms, then, may bestow an advantage to rare morphs (Clarke 1962a) or to the population as a whole (Moment 1962). In more general terms, such discontinuous variation may be classified as a type of 'protean behaviour' (Chance and Russell 1959, Humphries and Driver 1967, 1970) which proposes the existence of patterns of erratic behaviour whose function is to confuse predators. To the extent that the polymorphism is unsystematic, predators will have to learn that each morph represents food. The behavioural process of how they are believed to do this is known as the formation of a 'specific searching image'.

3. APOSTATIC SELECTION AND SEARCHING IMAGES

(a) Searching image

Croze (1967, 1970) suggests that hunting by 'searching image', a term coined by a naturalist (von Uexkull 1934), is more or less synonymous with the experimental psychologists' 'choice from sample' (Kohts 1923) and the human psychologists' 'matching by set' (Vernon 1952). These specialists have apparently named the same 'universal perceptual concept'. The common processes involved consist of three successive stages (Croze 1967, 1970): (i) 'seeing' the sample, (ii) examining the choice situation, (iii) reaction to the matching stimulus.

These three components can best be illustrated with reference to ourselves, for searching images are continually used in our daily lives. We become conditioned to looking for visual clues associated with some kind of reward. For example, a blue jug on the meal-table

may come to be connected with the idea that it contains milk, if in past experience, it has always been filled with this liquid. This psychological conditioning is equivalent to (i) above; seeing the sample. It is only when a choice situation (ii) is presented that the previous acquisition of a searching image becomes apparent. This may arise when, say, two jugs of milk are presented on the table; one the blue, as before, the other a jug of a totally unfamiliar design. Provided that the reward cannot be directly seen in either jug, the 'predator' will almost invariably take the familiar blue one; he is reacting to the matching stimulus (iii). The choice so made must be induced by the searching image per se, even if it is contrary to unlearned, innate preferences.

Von Uexkull (1934) was one of the first to recognise the possible existence of searching images, when he found that toads (Bufo bufo L.), fed on earthworms, subsequently snapped at matchsticks in a choice situation, and at ants or pieces of moss, after a diet of spiders.

The speed with which a searching image can be formed, and its specificity, is exemplified by the work of de Ruiter (1952) on the effectiveness of camouflage in the stick-caterpillar, Ennomos alcanara L. Caged hand-reared jays (Garrulus glandarius L.) and chaffinches (Fringilla coelebs L.) were used as predators. When sticks were added to the cages, the birds initially took interest in these new components of their environment and pecked at them. After the birds had become habituated to the twigs, dead caterpillars were also added. For a long time these went unnoticed, but once one was found (often by a bird accidentally treading on a caterpillar), others were also discovered. Initially, in their hunt for larvae, caterpillar-like twigs were also pecked, but the birds quickly became more efficient. This was even true for those experiments where the sticks were from the specific food-plant of Ennomos. Thus a searching

image can be extremely specific. As de Ruiter points out, however, birds in the wild would not have such a limited hunting area, and would have more time to habituate to twigs. His results, therefore, do not necessarily refute the camouflage hypothesis.

The literature contains other examples of work on searching images, mostly inspired by the painstaking ecological studies of L. Tinbergen (1960). These will be discussed later in relation to the evidence for apostatic selection.

(b) Searching images and colour polymorphism

Apart from the recent work of Arnold (unpublished), to be discussed later, virtually nothing is known about the behaviour of Cepaea-hunting thrushes. Certainly there is no direct evidence that they hunt this snail by morph-specific searching images, let alone preferentially search for the most common morph, as is required by the theory of apostatic selection. The same argument can be applied to all other non-mimetic polymorphisms.

Yet some supporting evidence for apostasy does exist. This will be examined in the next Chapter.

CHAPTER II THE EVIDENCE FOR APOSTATIC SELECTION

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1. INTRODUCTION

So far, attention has been concentrated on the problem of how colour-pattern polymorphisms are maintained. It has been pointed out that the visible distinctness of different morphs is suggestive of selection by predators hunting by morph-specific searching images. This characteristic carries little weight as evidence for apostatic selection when considered in isolation. It is the purpose of this Chapter to assemble and discuss the more conclusive findings that support the theory.

There are two main lines of evidence. The first is provided by considerations of the effect apostasis would have on two sympatric species exhibiting near-identical polymorphisms (Clarke 1962b). The second approach is more direct and concerns observations of predator-prey relationships.

2. MIXED COLONIES OF CEPAEA

A testable prediction can be made as to the effect of apostatic selection on two closely related polymorphic prey. It is essential for this prediction to be valid that the two species should: a. possess visibly similar polymorphisms, b. live in the same habitat, and c. share the same predators. If they satisfy these criteria, it is quite likely that predators would treat them both as the same species. This would mean that effectively one polymorphism would be maintained by predators selecting apostatically.

If a particular morph is at a high frequency in one species - for a reason unrelated to its visible properties, for example - then, if apostatic selection is acting, the same morph in the second species would be at an advantage only when present at a low frequency. The polymorphism would be brought to equilibrium at a point determined by the relative visibilities of the morphs against the background. Uniform backgrounds may produce an 'apostatic equilibrium point' with a high proportion of one phenotype in both species. In general, though, "a series of visually similar but ecologically diverse habitats should exhibit negative relations between the frequencies of equivalent forms in the two species". (Clarke 1962b). In the absence of apostasy, positive relations would be expected.

Strangely, the only species to have been investigated with regard to the above prediction are Cepaea nemoralis and Cepaea hortensis (Clarke 1962b, Carter 1967, Clarke 1969). A glance at the literature will reveal that the existence of negative relations is a matter of some controversy. Their presence was apparently revealed by a sequence of samples from 'open' habitats near Oxford (Clarke 1962b). Here there was a statistically significant negative correlation between the frequencies of yellow effectively unbanded shells in the two species. In woods there was also a negative correlation, though non-significant. Likewise, Carter (1967) has found similar negative relationships within habitat classes, but has questioned whether they are due to apostatic selection. In addition he has criticised Clarke's original data on a number of grounds, but without providing an alternative explanation for the negative correlations. A reply to Carter and a summary of the evidence for

apostatic selection are to be found in Clarke's (1969) paper.

Space does not allow a fuller discussion of the Clarke - Carter controversy, but it is evident that many more collections of mixed Cepaea colonies should be made before pronouncing the final verdict.

3. PREDATOR-PREY STUDIES

(a) Introducing the evidence

Until recently there has been a lack of direct research on apostatic selection and consequently much of its earlier support derives from other lines of enquiry. The evidence from Reighard (1908), Popham (1941, 1942) and L. Tinbergen (1960) are cases in point. Primarily as a result of the last author, new impetus was given to research by ethologists (e.g. Croze 1967, 1970; W. Tinbergen et al. 1967) interested in the behavioural aspects of predation and by population geneticists (e.g. Clarke 1962a, b; Arnold, unpublished) concerned with the implications of such behaviour to polymorphic prey.

Despite the diversity of its origins, the evidence falls into two groups. The first concerns experiments where predators feed solely on one particular prey before a choice situation. In the second, such 'training' is lacking. The distinction between these two designs is important, for though the first may reveal a mechanism for apostasy, whereby predators become accustomed to searching for one type of prey, the second compares more realistically with the natural situation. Here, predators have the chance of becoming conditioned to the first prey-types they encounter. According to the hypothesis of apostatic selection, they should on average become trained to the commoner types.

(b) Do predators become conditioned to searching for specific palatable prey?

Associative learning is a well-documented form of behaviour (see Thorpe 1956, Chap. IV). Predators, for example, rapidly learn to associate specific colour-patterns with distasteful prey and hence become conditioned to avoiding them. (See e.g. Blest 1957, Sexton 1959, Brower et al. 1960, Duncan and Sheppard 1964). The evolutionary importance of this type of behaviour cannot be disputed for it has led to the development of warning-coloration and mimicry in many unrelated species. Is the converse of this behaviour also true; can predators become conditioned to searching for palatable prey of a specific-colour pattern?

(i) General evidence

The classic work of Luuk Tinbergen (1960) provides an affirmative answer to this question. He showed, in a comprehensive ecological survey of titmice (Parus spp.), that birds can become so used to searching for a particular prey that later-emerging species are overlooked for a considerable time. All these prey were insect larvae, mainly of the Orders Lepidoptera and Hymenoptera, inhabiting pine trees. A variety of techniques, including direct observation of food brought by parent tits to their young, enabled Tinbergen to analyse the yearly factors determining the degree of larval predation. Although the density of the caterpillars was a principle component, their size, palatability and conspicuousness were also involved. By taking these into account he was able to study the effects of prey density alone.

When, for example, larvae of Acantholyda nemoralis and Panolis spp. first appeared in the tits' hunting environment, they constituted only a very small proportion of the food brought to the young. During the next few days their densities rapidly increased and then remained constant. Theoretically the tits should have quickly exploited such concentrations of larvae, particularly as these species were known to be highly palatable. Instead, there was a lag of about a week, on average, before the birds started to exploit the new food supply, whereupon the larvae suddenly appeared in the nestlings' diet. Tinbergen decided that these results could best be explained by assuming that the tits were hunting by searching image. When the larvae first appeared in the environment they were taken entirely by chance and hence infrequently; the tits were still searching for prey they were more familiar with. As the tits found more Acantholyda and Panolis, they were rewarded and gradually built up searching images specific to these prey. Total acquisition of these specific searching images led to the rapid increase in predation of the novel larvae.

Similar evidence for 'ecological' searching images has been provided by Hock et al. (1960) and Gibb (1962). All these studies contend that the formation of a searching image to a specific insect prey leads to an increase in its risk of predation. The important point to note, however, is that until this time the prey enjoys a certain amount of protection. If such behaviour is widespread among predators, it should be repeatable under laboratory conditions.

The earliest experimental evidence comes from Reighard (1908), working with the grey snapper Lutianus griseus (L.) as the predator and dyed sardines Atherina laticeps (L.) as prey. His aim was to test a now disproved hypothesis (see Lorenz 1962) for coral-fish coloration.

One hundred and fifty sea-caught snappers in a large outdoor pool were fed on about eighty sardines dyed blue. They were then given a choice of five blue and five unfamiliar (either normal, red, green or yellow) sardines. During presentation of the two colour-types Reighard noted the order in which the sardines were eaten. When blue and normal fish were offered, the latter type was understandably preferred. The remaining three tests revealed an overall preference for blue. Apparently the snappers had acquired searching images for blue-dyed sardines. Even in the face of a multitude of predators inhabiting an open pool, the other colour types were at an advantage, albeit short-lived.

Unfortunately, Reighard's apparent evidence for searching images may be doceptive. As Croze (1967) points out, blue was the only colour-type used for training the snappers. It is wrong to ignore the possibility that blue was a colour preferred as a result of learning unrelated to the training.

In a comparable experiment, Smith (1967) attempted to train individual minnows, Phoxinus phoxinus L., on one type of artificial prey (either white or black worm-like pieces of a mixture of lard and flour). One group of five fish was fed solely on the dark type whilst five other fish were given light prey. For three successive days, each minnow was given a thirty minute 'feeding period' on twenty monomorphic prey, scattered randomly on the sandy floor (2 feet x 1 foot) of an aquarium. Thirty-six hours after the last training period, each fish was presented with a 'population' of ten light and ten dark prey distributed at random within the tank. Subsequent observations of predation revealed that, on average, the minnows significantly favoured taking the familiar colour.

Similar results have been obtained by Beukema (1968) who has rigorously investigated the increases in risk of novel prey types when introduced to nine individual sticklebacks Gasterosteus aculeatus L. in an experimental tank under controlled conditions. The finding most relevant to the present discussion is that when the fish were accustomed to feeding on Tubifex worms, larvae of Drosophila were overlooked in preference to the former.

The experiments described above lend weight to the argument that predators continue searching for familiar prey when a novel type is introduced into the area of search. Such conditioning has been taken to an extreme by Rabinowitch (1961, 1968). In one experiment (1968), chicks of captive gulls, Larus argentatus and Larus delawarensis, were fed on one of three restricted diets. These were: chopped earthworms, pink cat-food and green cat-food. After five days of training each individual bird was offered a choice between first, the familiar food and one of the others, and second, between the two unfamiliar foods. In both species there was a very significant preference for the familiar diet. When confronted solely with unfamiliar food, some of the chicks totally refused to eat. Comparable results have been obtained by Capretta (1969) for chicks of Gallus gallus.

Rabinowitch's earlier (1961) experiments were even more dramatic. Six domestic chicks were reared on 'milo' from hatching and eight were similarly brought up on wheat. After six weeks the diets were reversed. So conditioned were they that two of the milo-trained and five of the wheat-trained chicks refused to eat the unfamiliar food and actually starved to death.

These results with young birds agree with L. Tinbergen's (1960) contention that a prey is not recognised as food until its reinforcing value has been established through experience. In this case, however, the avoidance of unfamiliar food was probably exaggerated as a result of the predators being at a highly impressionable age. A searching image should normally be more flexible, for it is to the predator's advantage if it can quickly switch attention to a particular prey.

The main stimulus involved in searching image behaviour appears to be the colour (or tone) of the prey. Dawkins (1966) has shown that domestic chicks will, on acquiring a searching image, hunt for prey on the basis of colour alone. Croze (1967) has demonstrated a similar effect in carrion crows, Corvus corone L. For example, when a white cockle covering a piece of meat was presented to a crow ('Abendago') on a beach, it subsequently turned over two white extraneous shells, a piece of white fluff, a broken white mussel shell and a dead rabbit in addition to seven white cockles, of the experiment proper, and a black stone. The latter incident was presumably an example of a chance encounter with an unfamiliar object (see page 34).

In another study Croze (op.cit.) enquired more deeply into the specificity of searching images. Crows were trained to overturn mussel shells painted red and distributed on a beach. In the choice situation, these were presented in equal numbers with another unfamiliar form. They were distinguishable from the standard shells by one of three criteria: colour, shape or surface structure. Generally, his results were that the chances of the unfamiliar form being taken depended on the degree of colour resemblance between it and the standard red shell. Thus red-yellow mussels were overturned as often as the

standard rods, whilst yellow mussels were totally overlooked. In comparison with colour, shape and surface texture were less important visual cues; red cockles, for example, were treated on equal terms with red mussels.

Until now, we have discussed the evidence only in relation to birds and fish, animals that mainly hunt by the sense of sight. It has recently been demonstrated that olfactive cues can also elicit searching images in predators. Soane (1970) has been able to condition captive rodents (Apodemus sylvaticus L. and Mus musculus L.) to search for artificial prey with a specific scent. During choice situations the familiar type was taken in preference to prey that had a different scent but identical appearance. Soane points out that there is scant literature on animal scent polymorphisms (but see Müller 1878 for scent dimorphism in the males of the butterfly, Battus polydamus). This situation may simply reflect lack of research. If future work reveals a wealth of animal species polymorphic for scent, then we must not overlook the possibility that such variation is being maintained by apostatic selection.

The main implication to be derived from all the findings discussed above is that predators may be capable of becoming conditioned to specific variants of a natural polymorphic animal. That this occurs, is, as will be seen, far from conclusive.

(ii) Natural polymorphic prey

The only polymorphic species that has been investigated in this context is Cepaea hortensis (Clarke 1961)¹.

Two pairs of hand-reared songthrushes were housed in separate sixteen-foot square cages. Each cage was divided into a straw-lined

¹Since the time of writing, the work of Don Boer (1971) has been published (see page 265).

'collecting-area' and a 'thrush-stone area'. Snails presented to the birds in the collecting area were taken to the thrush-stone site for breaking. Here the broken shells could be scored and counted.

The experiment involved only two phenotypes, yellow unbanded (Y00000) and yellow banded (Y12345) morphs. Possible errors from differences in taste and behaviour were minimised. For three days the birds were trained on yellow unbanded in one cage (cage I) and yellow banded in the other (cage II). They were then presented with 'populations' of the two morphs in unequal proportions:

260 Y00000's and 40 Y12345's in cage I
and 40 " " 260 " " cage II.

On each day, the broken shells were replaced by the same number of living snails with identical proportions of the two morphs. Hence the composition of the population was kept constant. The experiment was terminated when about 700 snails had been eaten. It was then repeated, the only difference being that the straw was slightly darker than before.

Clarke found no clear evidence of conditioning, since banded forms were preferred in every case, even when the birds had previously been trained on unbanded. In only one instance was the preference statistically significant; this was in the first experiment, cage I. When the results for both experiments in cage II were added together, banded forms were again significantly favoured. A possible factor contributing to these results is that the thrushes may have become very efficient at searching for Cepaea (cf. de Ruiter 1952) since this activity was virtually continuous (Clarke, personal communication). For instance, the shells may have been detected on the basis of tactile cues. These experiments have never been repeated.

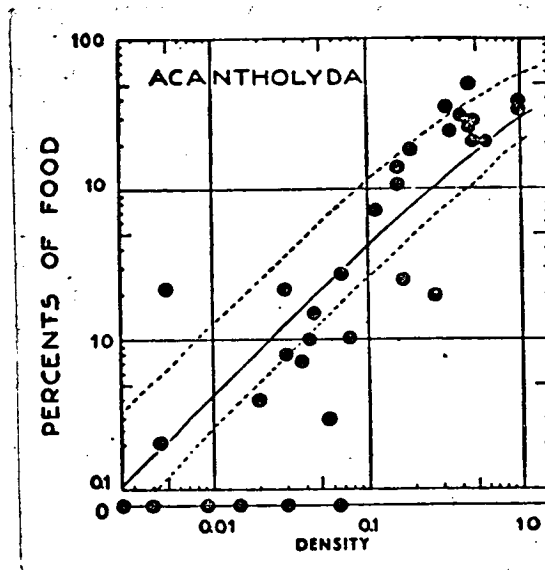


Figure 2

The relationship between the density of Acantholyda nemoralis and its proportion in the tits' diet. Note that at low densities the larvae were taken less often than expected (continuous line) and at high densities more often. From Clarke (1962a); his Fig.7.

(c) Do predators become conditioned to searching for the commonest types of a mixture of palatable prey?

We can conclude from the preceding discussion that predators may sometimes acquire searching images after several encounters with a particular type of palatable prey. If this prey is the commonest variety of a polymorphic species then selection will be apostatic. On the other hand, a rare morph may be the first type to be encountered by a naive predator. If the predator finds it unprofitable to hunt by using a searching image specific to this morph, it may possibly switch to searching for a commoner variety. Unless it does so, it will not select apostatically. We must now examine the literature for evidence as to whether predators do, on average, select in an apostatic manner.

(i) General evidence

Reference is again made to the work of Tinbergen (1960). Our interest centres on the situation when the tits were feeding on a number of larvae simultaneously. Tinbergen found that at low densities certain caterpillars were taken less often than expected. At moderate densities expectation was exceeded, whilst at very high densities tits prefer a varied to a monotonous diet and so dispense with searching images. Fig. 2 illustrates these findings, with regard to Acantholyda nemoralis.

Strictly, these data cannot be taken as evidence for apostasis, since Tinbergen was dealing with changes in density, not frequency (Croze 1967, 1970).

For genuine apostatic selection, as the density of Acantholyda increased, so the density of alternative prey should have decreased proportionally. This in fact did not always happen. Dr. J.N.M. Smith has drawn my attention to an additional criticism of Tinbergen's work (including the experiments mentioned on p.33). Predators probably deliberately seek out areas of local high prey density (see, for example, Goss-Custard's 1970 data for feeding by the redshank Tringa totanus L.). If the tits had acquired searching images for areas of high prey density (as opposed to for specific types of prey), then Tinbergen's estimates for overall prey density may not have been representative of the areas visited by the birds.

However, the work of Holling (1965) has also demonstrated similar responses to increases in prey density. He used captive small mammals, including deer mice, Peromyscus leucopus Rafinesque, as predators and cocoons of the sawfly Neodiprion sertifer Geoff. as prey. When alternative food was available, the number of cocoons taken by the predators varied with density in a manner similar to the response of tits to Acantholyda as shown in Fig. 2.

More experimental evidence comes from the work of Popham (1941). He investigated the selective value of crypsis in the corixid bug Arctocorisa (=Sigara) distincta L. Adults of these hemipterans can be various tones of brown, depending on the shade of the background on which the larvae develop. In one set of experiments two varieties were offered to rudd, Scardinius erythrophthalmus L. One of the morphs matched the underlying sand, whilst the other was non-cryptic. In each experiment different proportions of the two varieties were presented to the fish and these ratios were kept

Figures 3a and 3b

Clarke's reanalysis of the data from Popham (1941 and 1942). The Figures and Legends are taken from Clarke 1962a (Fig. 3a is equivalent to Clarke's Fig. 5 and Fig. 3b corresponds with his Fig. 6).

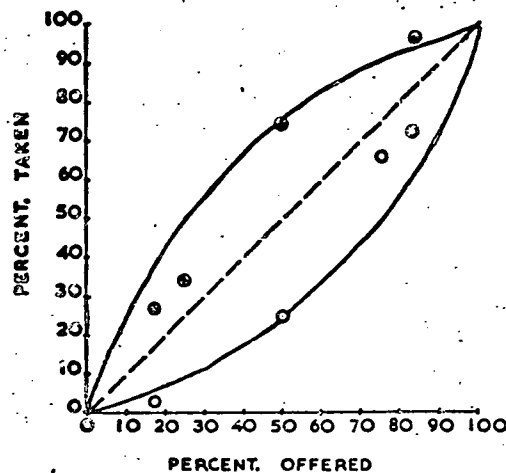


Figure 3a. The results of predation by Rudd Scardinus (Lousiacus) erythralis on corixid bugs Sigara distincta. In a series of experiments, two colour-types of bugs were offered to the predator in different proportions. The background was of uniform colour and tone ('i', on the Ostwald Colour Chart). The horizontal axis gives the proportion of any colour-type offered, the vertical axis shows the proportion taken by the Rudd. Open circles represent colour-type 'i' (cryptic) and crossed circles represent colour type 'i' (darker and less cryptic). Each experiment, which represents about 200 'predations', is therefore represented by two circles, one open and one crossed. For an explanation of the continuous and dotted lines, see text. Data from Popham (1941).

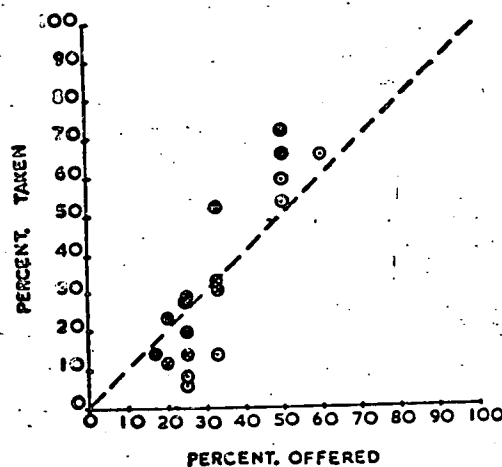


Figure 3b. A diagram similar to Fig. 3a., giving the results of another series of experiments in which an additional colour-type was introduced (colour-type 'n', even darker and less cryptic than 'i'). This is represented by the black circles. Note the change, in all colour-types, from advantage-ousness at low frequencies to disadvantageousness at high ones. Data from Popham (1942).

constant by replacing each eaten bug with another of the same colour.

Popham's data have been reanalysed by Clarke (1962a). The results of the first experiments are presented graphically in Fig. 3a. Clearly, the non-cryptic variety was over-predated at all frequencies. Using the data obtained from when the phases were presented in equal proportions, Clarke calculated the expected proportions taken from experiments involving unequal numbers of the varieties. These expected values are shown by the continuous lines in Fig. 3a. We can now see that the disadvantage of the non-cryptic morph decreased at low frequencies and increased at high. This effect was statistically significant.

In a second series of experiments (Popham 1942) when another variety of corixid was added to the system, there was again a definite advantage for a variety at a low frequency. Correspondingly, each type became significantly disadvantageous when relatively more abundant (see Fig. 3b).

Here appears to be clear evidence for apostasis. However the results were obtained from only three predators, and Popham himself showed that corixid bugs become restless when on a background of a colour differing from their own. These two factors may have imparted error to the experiments.

Smith (1967) carried out a set of experiments along the same lines as those of Popham. In this case, minnows Phoxinus phoxinus L. were presented with populations of dark or light artificial prey. He used large numbers of fish and offered different proportions of prey to each individual. Under such conditions, he was unable to duplicate Popham's results. This was apparently because the fish were so variable in behaviour; any apostatic component of selection

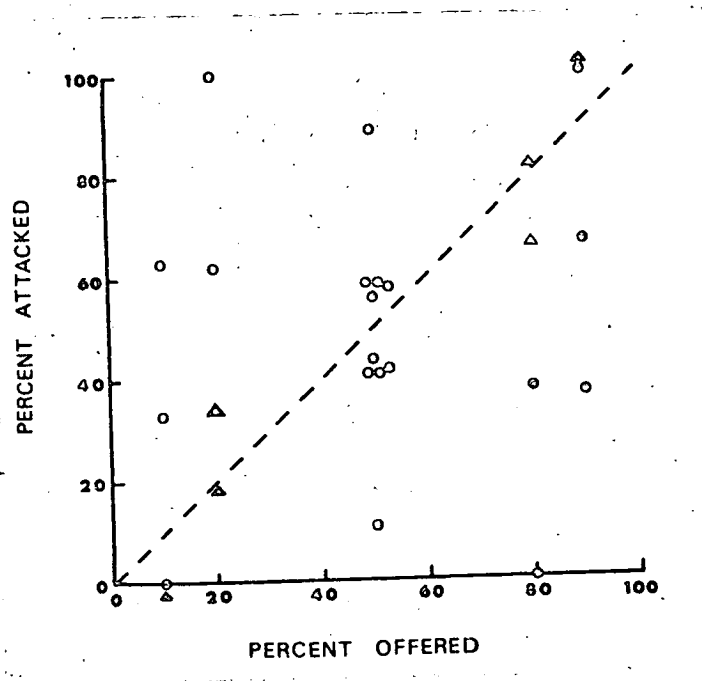


Figure 4

The results of predation by minnows (Phoxinus phoxinus) on dimorphic populations of artificial prey. Each trial is represented by two symbols, an open symbol designating the proportions of light prey offered and taken and a filled-in symbol denoting the percentage of dark prey offered and taken. The circles and triangles designate trials on two different backgrounds. Note the large variation in results compared with the expected values (dotted line). From Smith (1967).

would have been completely masked (see Fig. 4).

Individual differences in predator behaviour have also been shown by Pough (1964). In an attempt to test apostatic selection, he offered red and yellow painted sunflower seeds, in ratios of 9:1, to caged chickadees (Parus a. atricapillus). However, the heterogeneity in behaviour was not enough to conceal overall trends, for each bird tended to prefer the colour at the lower frequency. That is to say, the predators were behaving in a manner completely opposite to that predicted by apostatic selection. The prey were probably at too high a density. This point will be discussed in more detail later (see Chapter IV).

(ii) Natural polymorphic prey

We are again forced to turn to Cepaea, the only species that seems to have been satisfactorily investigated in the present context. Reference is made to some unpublished experiments carried out by Dr. R.W. Arnold (personal communication). He set up artificial colonies of Cepaea nemoralis at different sites in beech woods. These populations each contained over 1000 snails and differed from one another with regard to the relative frequencies of the morphs that they contained. Only two varieties were presented: unbanded yellows and unbanded browns. Thrushes regularly visited the populations and their anvils were periodically visited in order to assess the predation. Yellows were always taken to excess. That is, relatively too many yellows were taken from populations where this colour was presented at low frequencies as well as from populations where yellows were common. But by taking this preference into account, Arnold was able to show that selection was in

fact frequency-dependent.

4. CONCLUSIONS

From the preceding review of the evidence, three main conclusions can be made with regard to:

- (a) conditioning to a specific prey;
- (b) the specificity of conditioning;
- (c) apostatic selection.

(a) Conditioning to a specific prey

Sight-dependent predators can, under certain conditions, become accustomed to searching for a prey of a particular colour or pattern. The frequency with which this occurs in nature is unknown; few of the experiments described concerned predators in their every-day environments. Of these studies, the evidence from Tinbergen (1960), Mook et al. (1960), Gibb (1962) are least reliable since selection may have been based on other cues besides the colour or pattern of the insect prey. The most satisfactory data are those from Croze (1967, 1970).

(b) The specificity of conditioning

Apart from the work of Croze (1967, 1970) little is known about the specificity of this conditioning. Yet this is of crucial importance, since the theory of apostatic selection assumes that predators acquire morph-specific searching images. Attempts at conditioning predators to a particular morph of Cepaea have failed (Clarke 1961), though the occurrence of such conditioning is implied from the results of Arnold (unpublished) and from Clarke's (1962b) work on mixed colonies of Cepaea species.

(c) Apostatic selection

Even if sight-dependent predators do, in fact, become conditioned to searching for a particular variety of a polymorphic prey, there is no logic in assuming that they select apostatically. Yet it is critical to the theory that, overall, they should hunt for the commoner varieties. Arnold (unpublished) has provided the only satisfactory demonstration that predators (individually or overall) select prey in a frequency-dependent manner.

The next Chapter discusses the basic techniques that were used in experiments designed to investigate the above and other related topics.

CHAPTER III GENERAL MATERIALS AND METHODS

CHAPTER III GENERAL MATERIALS AND METHODS

O blackbird! sing me something well:
While all the neighbours shoot thee round,
I keep smooth plots of fruitful ground
Where thou mayst warble, eat and dwell.

(Tennyson 1842).

1. INTRODUCTION

This research was specifically aimed at testing apostatic selection, and in this respect differs from most of the work discussed in the previous Chapter. The approach to the problem was basically simple: wild birds in their natural surroundings were offered populations of polymorphic artificial prey.

2. CHOICE OF EXPERIMENTAL SYSTEM

It must be remembered that experimental conditions, especially in the case of animals in captivity, may distort responses to the prey. In the present experiments the birds were in their usual habitats (gardens or fields) and were therefore subject to environmental influences outwith the experiments per se. In this respect the method differs from those involving caged birds and is nearer the natural situation.

Ideally, predators should be directly observed feeding on polymorphic prey in the field. Unfortunately, accurate observation and identification are difficult under such conditions. Predators are active creatures; a meadow-pipit feeding on Philaenus in long grass, for example, would probably capture and swallow its prey almost instantaneously. Even assuming he saw this act an observer would have great difficulty in identifying the species of prey caught, let alone its variety.

An improvement on this approach is to present predators with

artificial populations of their natural polymorphic prey. In this way the site of the experimental population can be controlled and can be so designed as to be fully observable to the researcher. Problems of practicality are, however, still involved. An important potential source of error concerns the possible relative behaviour (e.g. mobility) of different morphs. This might be overcome by killing the animals before presentation, but most wild predators do not normally eat their usual prey that are already dead. Katz (1937) tells of frogs that starved by the side of a heap of dead flies; they did not recognise the motionless insects as edible. In zoos, penguins are usually fed on dead fish. During eighteen years of observations on king penguins (Aptenodytes patagonica) Gillespie (1932) did not note a single case of them taking a fish from the ground. At feeding time every bird had to be fed singly by hand.

It was decided, therefore, to employ artificial polymorphic prey. These are immobile and 'novel' and have the added advantage that they can be made desirable to many species of birds. Moreover they overcome the problem of obtaining large numbers of specified phenotypes.

Ground-feeding passerines are ideal for prey-selection experiments. Apart from their abundance and ubiquity, their main assets are that they hunt almost exclusively by sight and possess colour vision (Pumphrey 1948, Kettlewell 1955) and are extremely efficient at searching for prey (cf. Heppner 1965, for Turdus migratorius). Many passerines undoubtedly feed on polymorphic prey in the wild.

3. BIRDS

The species of birds involved are some of those normally to be found feeding on lawns or fields. A full list is given in Table 1. Further details of feeding habits and general behaviour can be found in Witherby et al. (1938).

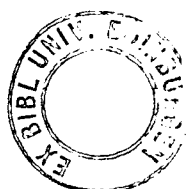


Table 1

List of birds involved in experiments

Common name	Scientific name
Blackbird	<u>Turdus merula</u> L.
Songthrush	<u>Turdus philomelos</u> Hart (= <u>T. ericetorum</u> Turton.)
Robin	<u>Erithacus rubecula</u> Hart.
Dunneck (hedge sparrow)	<u>Prunella modularis</u> Hart.
House sparrow	<u>Passer domesticus</u> L.
Starling	<u>Sturnus vulgaris</u> L.
Blue tit	<u>Parus caeruleus</u> L.

Table 2

Colours of the green and brown baits, based
on the Munsell Colour System (1966)

	Hue	<u>Value</u> Chroma
Green	7.5 GY	$\frac{7}{10}$
Brown	5 YR	$\frac{6}{6}$

Note. The hue of a colour indicates its relation to red, yellow, green, blue and purple; the value its relative lightness or grey value; and the chroma, its strength.

The most important predator was the blackbird (for its habits, see Snow 1958). This was always the first, and sometimes the only, species to feed on the experimental populations. In general, additional species participated in experiments carried out on lawns or in market gardens, in urban and suburban areas. On the other hand, all the studies performed in rural fields involved blackbirds alone.

4. PREY

In most experiments, the prey were green or brown cylindrical pellets, 0.7 cm long X 0.7 cm wide and a description of their appearance and manufacture now follows. Other types of prey will be discussed in the relevant Chapters (IV and IX).

(a) Morphology

The morphs differed only in colour. Plate 1 to some extent illustrates this contrast, whilst Table 2 lists the differences more precisely by giving the scores of the two colours according to the Munsell Colour System (1966). Green and brown were chosen for the original experiments (Allen 1967, and see Chapters V and VI) because it was believed that they would be representative of natural palatable foods. The results of these experiments dictated that the same colours should be employed in most of the ensuing work.

With regard to other properties the morphs were apparently identical. The baits were of a manageable size for both experimenter and birds; from my point of view they could be easily handled, and most passerines could swallow them whole. Care was taken to ensure that the prey (or 'baits') were made of approximately equal size.



Plate 1

2 standard brown and 2 standard green
baits on a grass lawn. Each bait is
0.7 cm (approx. $\frac{1}{4}$ ") in length.

There was no evidence for large differences in taste (see Chapter IV).

(b) Manufacture

The prey were made from plain flour ('Snowy Mountain') and lard ('White Cap') in a 5 to 2 ratio by weight (after Turner 1961). Kneading produced a malleable dough of 'plasticine'-like consistency. Artificial food dyes (varieties 'green' and 'brown', supplied by the Scottish Colour and Flavour Company) were then added, 11cc of dye per 1000 gms of dough giving the required colours.

Once the kneaded mass of dough had attained a uniform coloration, it was forced by hand through holes (0.7 cm diameter) drilled in a sheet of perspex. The long 'worms' so-formed were laid side-by-side and simultaneously chopped into 0.7 cm-long sections. Large numbers of baits were made at a time and were stored in plastic boxes at room temperature until required.

5. ENVIRONMENTS

As already mentioned, the experiments took place in gardens or fields. The background was usually grass, though in some cases soil was used (see Chapters V and VI). To the human eye, browns appeared slightly more conspicuous against grass, while greens were slightly more conspicuous against soil (pp. 118-119). Rain dulled the colours and made the baits soft and mushy, causing them to disintegrate, so that they had to be frequently replaced. There was no evidence that wet baits were treated any differently from dry ones.

Experiments at different sites had different environmental variables and these were often correlated with climatic conditions. The birds (with regard to both species and individuals) were not necessarily the same at any two or more given sites and, in general, predators may be more selective in summer than in winter (cf. Prop 1960). The background at different sites also differed; the well-mown grass of a summer lawn

is a more uniform substrate than, say, a winter field.

Variation also occurred within experiments. There was no guarantee that the composition of predators was the same at any two points of time within a given experiment (e.g. see p. 96), unless the birds were colour-ringed (e.g. see Chapter VII). Fluctuations in background conditions were also liable to occur, particularly in summer, because of mowing, rain or drought. The last two variables affected the overall colour of grass, but the differences within each experiment were slight. Rain only prevented birds from feeding when it was very heavy. Snow lay on the ground during parts of some of the experiments described in Chapter VI, but the effect of this variable was remarkably slight (see pp. 118-119).

In other words, the bait populations had many variables in common with natural prey populations. We shall return to some of them at later stages. Despite the environmental differences between experiments, the results were often strikingly similar.

6. TECHNIQUES

(a) Presentation of prey

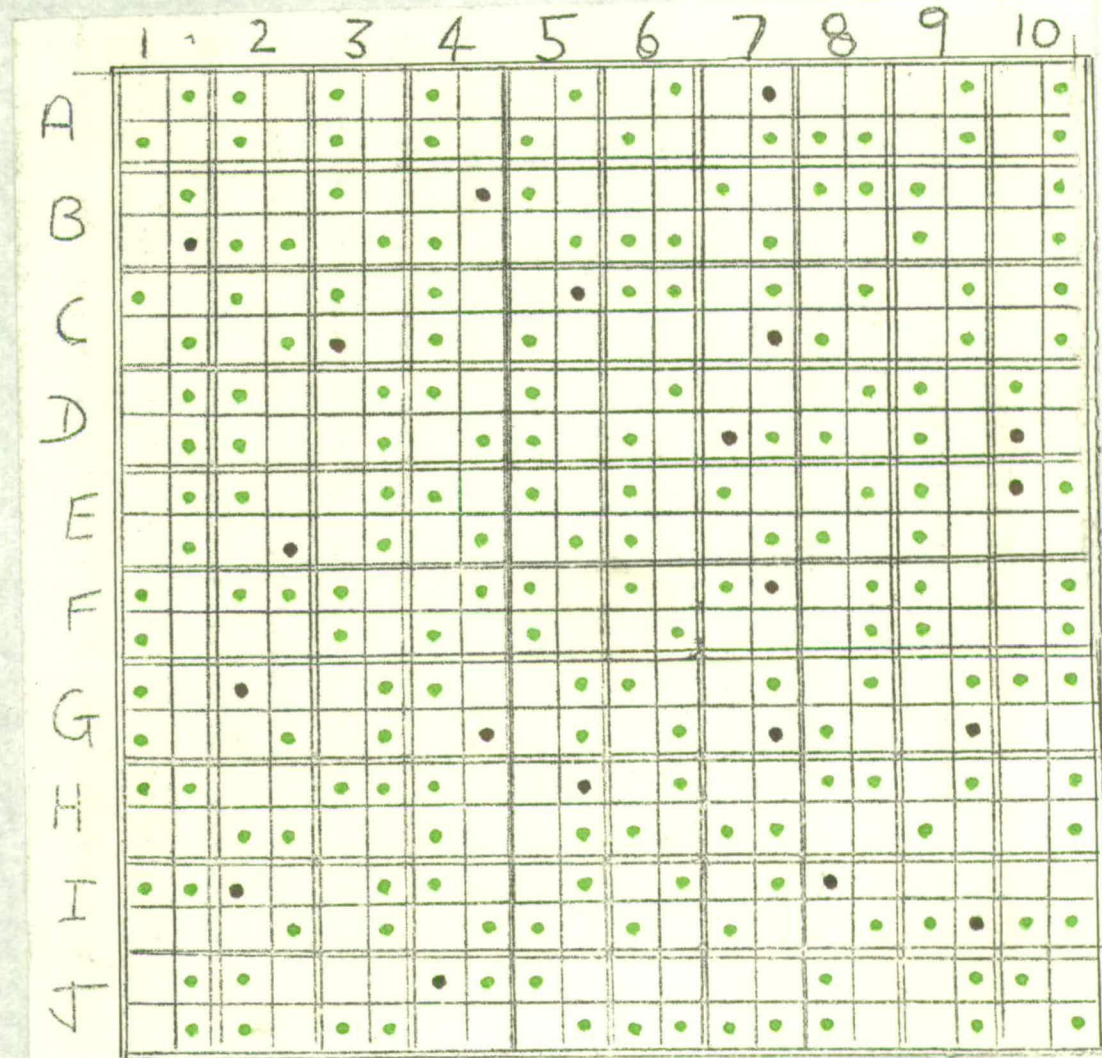
At some stage in each experiment a population of randomly distributed prey was presented to the birds. The baits were usually at a density of two per square metre (for the exceptions see Chapter IV) and the procedure of establishing one such population was as follows:

(i) Experimental plot

First, the area to contain the population was marked out. This comprised a rectangular or square grid of one-metre squares delineated by metal or wooden skewers. Each column and row was respectively numbered and lettered by upright skewered cards around the perimeter and, in

Figure 5

'Roneo'-copy of grid used on 22.4.69 in experiment 5.5, Chapter VI, showing the distribution of 180 greens and 20 browns. The squares with double lines represent the one-metre squares of the plot. Skewers were placed at points equivalent to the intersections of the double-lines. The four quadrants of each metre-square are also shown. For details of the randomization of the spatial distribution, see text.



some cases, along the middle lines. This facilitated identification of each metre-square. Physical and practical factors limited the size of the plot but generally it was 100 square metres, corresponding to a population size of 200 baits.

(ii) Randomization of prey distribution

The randomness of the distribution of the prey was an important component of the experimental system and the methods by which it was attained deserve full discussion. The first stage was to make 'Roneo'-copies of the grid (Fig.5) with each metre-square divided into four quadrants. These copies were then used to record the distributions of the future populations. Randomization of a given population was carried out in two stages, as follows:

First, the baits were randomized with respect to position. The four quadrants of each metre-square were labelled clockwise from 1 to 4 and then from 5 to 8. Thus each quadrant was represented by two numbers. Tables of random numbers (Fisher and Yates 1963) were now employed. Different rows or columns of these tables were used for each distribution. As the random numbers were read, the sequence of occurrence of the numbers 1 to 8 gave the spatial distribution of the baits. The following points were observed:

- A. The copy of the grid was filled in row by row.
- B. The positions (with respect to quadrants) of two baits were marked per metre-square.
- C. These two baits were never positioned within the same quadrant. This necessitated the rejection of random numbers that followed one designating the same quadrant.
- D. Random numbers 0 and 9 were ignored.

Once the future positions of the baits had been established, their

distribution with respect of colour was computed. In the early experiments random numbers were used. For instance when two colours were to be presented in equal proportions (e.g. see Chapter V), half the random numbers (0-5) designated one colour, say green, and the rest (6-9) represented browns. The colours of the baits were then superimposed on their positions according to the order of the random numbers that were read. However this procedure frequently resulted in discrepancies from the required proportions, and the colours of some of the baits therefore had to be changed. This process required further randomization.

In order to quicken the operation later experiments involved the use of playing cards. Thus in '1:1' experiments, equal proportions of cards of red and black suits were employed. One colour represented green and the other brown. Care was taken to ensure that the cards were thoroughly shuffled before use. They were dealt one by one and the ensuing order of the colours was systematically superimposed on their positions shown in the plan.

During the preliminary experiments it was discovered that the plots may not be searched uniformly by the birds; for instance, they may prefer one particular corner. These birds would be exposed to the morph-frequencies only within this particular area and such frequencies might differ from the proportions within the population as a whole. In order to combat this possible source of error, the grids of later experiments were divided into four equal areas. Each of these sections contained identical proportions of the morphs. Thus in the case of populations with equal numbers of greens and browns, each of the four areas had baits in ratios of 1:1. This procedure minimised the possibility of large differences in morph frequencies between different parts of the population.

Using the plan as a guide, the prey were now spread within the

grid. To eliminate possible bias in the positioning of baits relative to ground cover, they were dropped into their appropriate quadrants from waist height. Further randomization was added to the system by frequent changing of the distribution. This was usually carried out daily and ensured that the birds were unable to learn the positions of the baits.

(b) Recording of data

Each population was observed from suitable cover; for example, a room or a 'Land-Rover'. Binoculars were essential for watching the behaviour of the birds. When a bird entered the plot, the events were chronicled in the following order:

(i) Time of entry.

(ii) Species of bird involved and, if possible, its sex, the colour of its ring (see Chapters VII, VIII and IX), and other recognition marks.

(iii) Positions of baits 'eaten' or 'imprint-pecked'. This was done by tracing the paths of each bird on to the plan and thus marking the positions of the relevant prey. If all or part of a bait was eaten it was defined as 'eaten'. But if it was picked up and then dropped it was defined as 'imprint-pecked' (see Chapters VII and VIII) and 'uneaten'.

(iv) The colour sequences of baits eaten and imprint-pecked (actually recorded under (iii)).

(v) Other points of interest, for example behavioural aspects relevant to feeding.

(vi) Time of departure. This was rarely possible to record accurately when more than one bird was feeding.

With practice, two or more birds could be observed simultaneously but when predation became too heavy only a few selected individuals could be followed. The overall proportion taken by the rest was

deduced by subtracting the numbers of observed eaten baits from the total numbers actually missing.

All experimental populations were at some stage observed in the above manner, but some (see Chapter VI) were also subjected to 'unobserved' predation. This simply means that they were left unattended for a few hours and then examined on return, in order to determine the proportions taken.

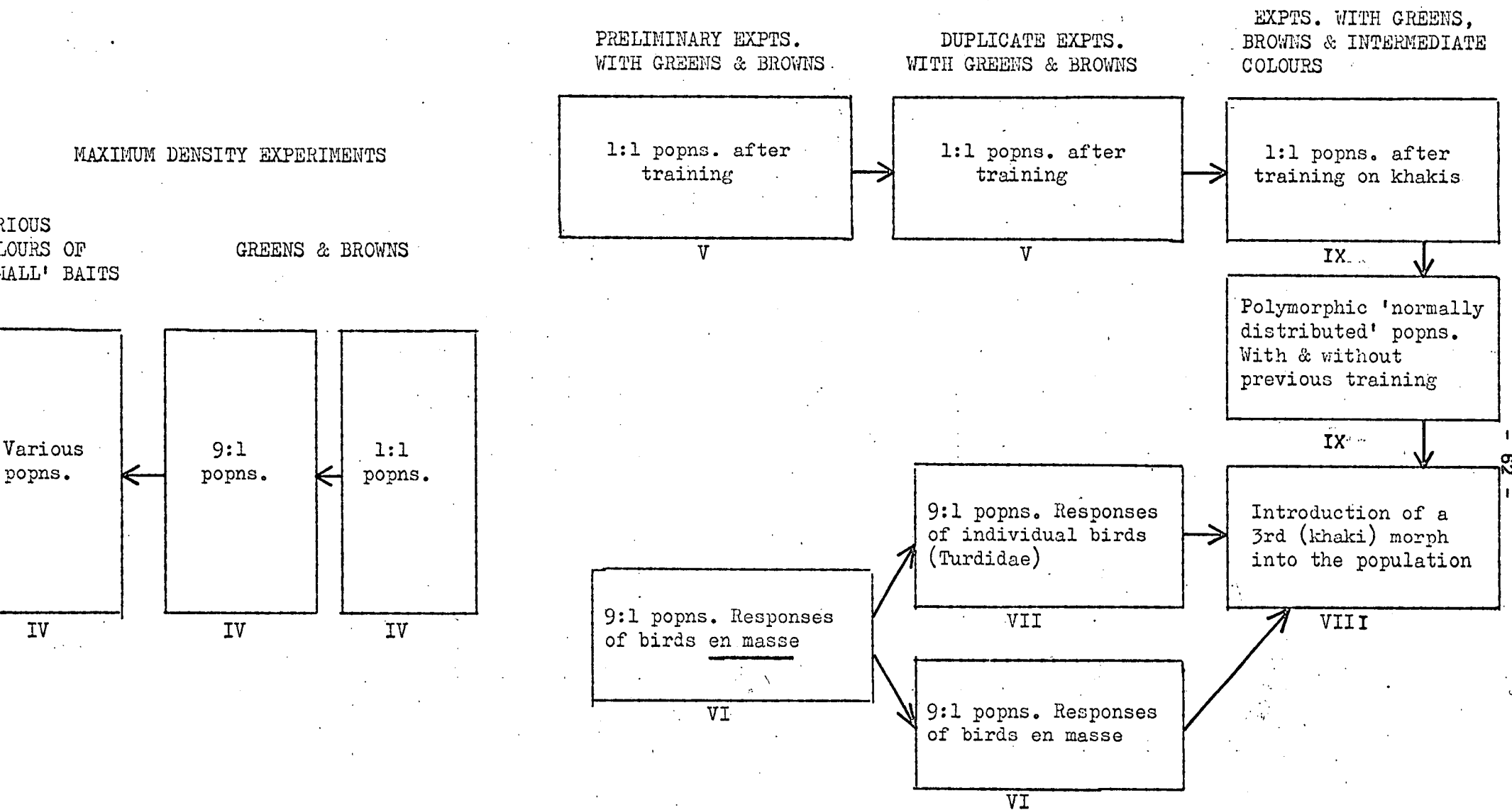
7. PLAN OF EXPERIMENTS

The campaign to test apostatic selection evolved along two main pathways. The first involved determining whether birds can become conditioned to search for a particular colour (see Chapter II, pp.33 -39). Wild passerines were fed on either greens or browns and were then presented with a mixture of both in equal proportions. After a preliminary experiment, a series of duplicates was carried out. Later experiments were designed to test the specificity of conditioning. These last studies involved the presentation of additional colours of various shades of khaki.

The second approach was to discover whether untrained birds preferentially search for the commoner colour in a mixture of two morphs (see Chapter II, pp.40 -47). Populations of greens and browns, with one colour nine times as common as the other, were presented. These '9:1' experiments were repeated a number of times and results were obtained for selection by both individual birds and groups of birds.

Finally, the two strategies converged on experiments involving the presentation of 'normally distributed' polymorphic populations containing greens, browns and various shades of khaki.

Figure 6. Interrelations of Chapters IV to IX.I



All these populations were presented at densities of two baits per square metre. In an additional set of experiments populations were offered at much higher densities. One of the aims of this study was to test 'unifying' selection (Pielowski 1959) which, in effect, is the opposite of apostatic selection.

Figure 6 summarises the evolution of the work and relates the experiments to each of the following five Chapters. It should assist the reader to visualise the connexions between the several major types of experiments. Of these, we first describe and discuss those that were carried out at high densities.

CHAPTER IV MAXIMUM-DENSITY EXPERIMENTS

CHAPTER IV MAXIMUM-DENSITY EXPERIMENTS

1. INTRODUCTION

This Chapter describes experiments with dense populations of baits. Consider the case of birds feeding from a bowl containing a mass of standard greens and browns in equal proportions. If predation departs significantly from the expected 1:1 ratio then it can be assumed that for some reason one morph is relatively more attractive than the other. Let us now imagine that the colours are presented in unequal proportions with, for example, greens nine times as common as browns. By taking the frequency-independent colour preferences into account we can derive values for the expected predation. If apostatic selection acts at such high densities then the birds should take relatively more greens than expected.

However, the literature contains evidence suggesting that the opposite is the case: rare types are likely to be picked out from a group. For example, Pielowski (1959 and 1961) has shown that goshawks (Accipiter gentilis L.) take white pigeons more often when most of the flock is black, and black ones more often when most of the flock is white. Similar results have been obtained for other predator-prey systems by Tinbergen (1946), Willard (1966, quoted by Salt (1967)) and Pough (1964). The experiments carried out by the last worker were supposedly designed to test apostatic selection and will be discussed later in the Chapter.

The main aim, then, was to discover just how wild birds respond to populations containing baits at very high densities and in unequal proportions. This line of inquiry progressed from using standard greens and browns in the first series of experiments to employing



Plate 2

Maximum-density experiments (series 1). Population 1a: 150 standard greens + 150 standard browns randomly distributed within a metal sieve 19 cm in diameter.



Plate 3

Maximum-density experiments (series 2). 1:1 populations: on left, 70 small greens + 70 small browns; on right, 70 small reds + 70 small yellows. The petri-dishes are 9 cm in diameter.

smaller baits of those and other colours, in the second.

2. MATERIALS AND METHODS

(a) Series 1

The populations of standard green and brown baits were presented in circular (19 cm diameter) metal sieves, an arrangement that ensured that water did not collect. In late March 1968, 150 green and 150 brown baits were randomly distributed within a sieve (Plate 2), which was then placed on the edge of a lawn outside the Department of Zoology, University of Edinburgh. The baits were very closely packed; in fact they were at the maximum possible density for objects lying on a plane surface. Periodically, this population (1a) was examined and, after recording the numbers of baits taken, was reconstituted to its original size. Frequent observations from the adjoining building determined that the sole predators were blackbirds, probably just a male and his mate.

After 6 days of presentation, and an interval of about two weeks, the 1:1 population was replaced by two others of the same size; one with greens nine times more common than browns (1b) and the other with browns nine times as common as greens (1c). The sieves containing these populations were placed one metre apart and their positions relative to one another were frequently and randomly changed. In other respects the experiment was carried out as before. During the eighth day, the blackbirds were joined by an indeterminate number of house sparrows and the rate of predation rose accordingly. The experiment lasted over a month.

(b) Series 2

The advent of predation by house sparrows during the last experiment

introduced a source of error. These birds tended to peck the baits rather than eat them whole and small pieces were consequently left in the sieves. These were roughly reconstituted into whole baits in order to derive an estimate of the numbers of whole baits eaten.

In the experiments that ensued, this problem was overcome by presenting baits of such a size that house sparrows could swallow them whole. These baits were round (approx. 0.3 cm diameter) pellets which were made from small pieces of coloured lard and flour moulded between thumb and forefinger. In experiment 2a they were green and brown, as before, whilst in 2b they were yellow and red (see Table 3 and Plate 3).

Table 3. Scored by the Munsell Colour System 1966 (see p. 52) the reds and yellows had values as shown.

	Hue	$\frac{\text{Value}}{\text{Chroma}}$
Yellow	5Y	$\frac{7}{10}$
Red	7.5 RP	$\frac{5}{10}$

The populations of these baits were presented in circular (9 cm in diameter) plastic petri-dishes with small holes drilled in their bases for drainage. Each dish held 140 baits and the dishes were presented in a straight line and placed 50 cm apart. During the experiments the populations were maintained as before. Experiment 2a was started on 10th May 1968, when 1:9, 9:1 and 1:1 populations were offered to the birds. After four days, 7:1 and 1:7 populations were added and the experiment continued for four more days. Experiment 2b started on 20th May 1968 and followed the same plan as its predecessor.

Table 4

Grand totals of green and brown baits taken from populations
presented during experiment 1.

Proportions offered	Dates (1968)	Predation	
		G	B
1a. 1G:1B	31.3 - 6.4	202	226
		Expected 1:1	214 214
1b. 9G:1B	22.4 - 27.5	1606	592
		Expected 9:1	1978.2 219.8
		Expected constant selection	2027.7 170.3
1c. 1G:9B	22.4 - 27.5	743	942
		Expected 1:9	168.5 1516.5
		Expected constant selection	215.9 1469.1

3. RESULTS

(a) Series 1¹

(i) Synopsis

Table 4 gives the grand totals of baits taken from the 1:1 and two 9:1 populations of standard greens and browns. The values for expected predation, assuming random selection, are also shown. The results for the 1:1 experiment suggest a slight preference for brown but the deviation from expected is not significant ($\chi^2_{(1)} = 1.35$, $P > 0.20$). On the other hand, both the 9:1 populations suffered heavy overpredation of the rarer morph. These deviations from expected are very highly significant (when brown was rare, $\chi^2_{(1)} = 700.30$, $P < 0.001$; when green rare, $\chi^2_{(1)} = 2176.40$, $P < 0.001$). Clearly, the birds were exercising selection against the rarer colours and this was of such a magnitude that it overrode any selection due to frequency-independent colour preferences.

Nonetheless, another type of selection is in fact, detectable. The two populations containing the colours in unequal proportions were carried out simultaneously and should have been subjected to identical environmental influences, including numbers of visits by predators. It is valid, therefore, to compare directly the data collected from experiments 1b and 1c. If this is done, we find that as well as preferring the rarer baits, the birds tended to take green ones. This tendency can be detected by comparing the proportions of common and rare baits taken from each population. The null hypothesis is that these ratios are the same, assuming constant selection against the rare forms. This is not the case ($\chi^2_{(1)} = 124.51$, $P < 0.001$). It can be deduced from the data that this heterogeneity is due to the

¹Some of these results have now been published (Allen 1972).

Table 5

Numbers of baits taken by male (♂) and female (♀) blackbirds during observed visits in experiment 1a.

Date	Time of observation (B.S.T.)	Numbers taken		
		G	B	
31.3.68	19.01	0	3	♂
2.4.68	14.00	12	0	♂
	18.40	13	0	♂
	11.10	1	3	♀
3.4.68	11.29	2	0	♂
	11.31	7	0	♂
	9.30	0	17	♂
4.4.68	9.31	3	0	♀
	9.29	1	4	♂
Grand totals		39	27	

predation of relatively too many greens from both populations.

We can show that this preference has, indeed, little effect on the general frequency-dependent findings described above. If selection remained constant for the duration of 1b and 1c then the cross-product ratio:

$$\frac{\text{no. of browns taken} \times \text{no. of greens offered}}{\text{no. of greens taken} \times \text{no. of browns offered}}$$

should be the same in both experiments. The average C.P.R. gives a measure of the relative preferences: C.P.R. = 0.756, which indicates that greens were the favoured prey. Taking this into account we can derive the expected numbers of baits taken. Reference to those values, shown in Table 4, reveals that selection against the rarer morphs is still excessively heavy ($\chi^2_{(1)} = 1131.58$, $P < 0.001$ for experiment b and $\chi^2_{(1)} = 1475.87$, $P < 0.001$ for experiment c).

(ii) Behaviour of the birds

The findings yielded by examination of the grand totals for each experiment are supported by the data collected during the periodic observations. Blackbirds accounted for all the observed predation in 1a and for most of it in 1b and 1c. This is illustrated by Tables 5 and 6 which give the numbers of baits taken per visit during experiments 1a and 1b/ 1c respectively. Altogether, the observed birds removed approximately equal proportions from the 1:1 population and, when feeding on the other populations, they tended to take the rare colours, despite an omnipresent preference for greens.

With regard to experiment 1a, if selection at each visit had been random, we would expect the baits to have been taken in approximately equal proportions. This was clearly not the case. The results appear to be very heterogeneous, though they are not

Table 6

Numbers of baits taken by male (♂) and female (♀) blackbirds and house sparrows (HS) during observed visits in experiments 1b and 1c.

		expt. 1b 9:1 = G:B		expt. 1c 1:9 = G:B	
Date	Time of observation (B.S.T.)	Numbers taken		Numbers taken	
		G	B	G	B
22.4.68	11.40	5	0		
"	14.45			1	0
23.4.68	16.24			1	0
"	20.34	0	7		
24.4.68	11.46			2	0
26.4.68	14.45	2	0		
30.4.68	10.32			5	0
1.4.68	11.10	2	0		
7.4.68	15.25			2	0
"	15.28			3	0
"	15.38			0	7
9.4.68	11.00			4	0
"	16.10	2	0		
10.4.68	16.50	0	5		
12.4.68	17.30	3	0		
"	"	2	0		
"	17.42			0	1
"	"			1	0
"	"			1	0
"	"			1	0
13.4.68	12.00			1	0
"	14.10	1	0		
14.4.68	10.00			3	0
15.4.68	11.01	4	0		
"	16.52	1	0		
16.4.68	10.03			3	0
"	10.42			2	0
17.4.68	11.15	0	2		
"	11.18	0	2		
"	11.20			0	3
18.4.68	11.30	8	0		
"	"			4	0
"	"	4	0		
"	12.15	1	0		
19.4.68	11.15	8	0		
20.4.68	14.45			1	0
23.4.68	10.02			3	0
"	10.03	3	0		
"	"	1	0		
"	"	1	0		
26.4.68	"	0	11		
Grand totals		48	17	40	11

* The data for 11.30 B.S.T., 18.4.68, represent three consecutive visits by the same female blackbird

amenable to analysis by chi-squared. Indeed, on only two of the nine visits did a bird take both types of prey. Thus after selecting a first colour, a bird would tend to continue picking out the same type.

These differences of behaviour were even more pronounced in the subsequent experiments (see Table 6). The results from forty-one visits are shown. On average, at each visit, we would expect baits to have been taken in the ratio of 48 greens to 17 browns in experiment b and 40 greens to 11 browns in experiment c. In fact not one of the visits involved predation of both colours. Again we can presume that once a bird picks out a colour, it continues to select it. Even when a bird visited both populations, as on 18.4.68, it still continued to choose greens from both, although in one population this type was rare and in the other common.

(b) Series 2

The data obtained from these experiments support the main findings described above. Tables 7 and 8 summarise the numbers of baits taken in experiments a and b respectively and Figs. 7 and 8 present these results graphically by comparing, for each population, the proportions taken with the proportions offered.

The results will firstly be treated by assuming that selection from each population was random. With regard to experiment 2a, it follows that too many of the rare colours were removed from each of the four populations containing the morphs in unequal proportions. In three of them the effect was highly significant. Taking all four together, there was a significant tendency to take the uncommon colours ($\chi^2 = 23.03, P < 0.001$). Predation on the 1:1 population

Table 7

Grand totals of green and brown small baits taken from populations presented in experiment 2a. Predators were blackbirds and house sparrows.

Prepns. offered	Predation		Expected predn. (no selection)		$\chi^2_{(1)}$	P
	G	B	G	B		
1G:9B	212	362	57.4	516.6	462.66	<0.001
3G:7B	155	175	99.0	231.0	45.25	<0.001
1G:1B	260	282	271.0	271.0	0.89	NS
7G:3B	202	99	210.7	90.3	1.29	NS
9G:1B	382	174	500.4	55.6	280.14	<0.001

Table 8

Grand totals of red and yellow small baits taken from populations presented in experiment 2b. Predators were blackbirds and house sparrows.

Prepns. offered	Predation		Expected predn. (no selection)		$\chi^2_{(1)}$	P	Expected predn. (on basis of 4:1 results)		$\chi^2_{(1)}$	P
	R	Y	R	Y			R	Y		
1R:9Y	79	152	23.1	207.9	150.30	<0.001	35.1	195.9	64.70	<0.001
3R:7Y	53	81	40.2	93.8	5.82	<0.02	54.8	79.2	0.097	NS
1R:1Y	142	88	115.0	115.0	12.68	<0.001	-	-	-	-
7R:3Y	84	58	99.4	42.6	7.95	<0.01	112.2	29.8	33.74	<0.001
9R:1Y	260	81	306.9	34.1	71.67	<0.001	319.0	22.0	169.40	<0.001

was not significantly different from expected.

The birds responded to red and yellow baits in a similar fashion. Again, in 2b, the four relevant populations all suffered excessive predation of the rare colours and in each case this effect was significant. On the other hand, selection from the 1:1 population also differed significantly from expected.

Apparently, then, selection was frequency-dependent in both experiments, that is if we assume that the birds were expected to take the baits in the same proportions as presented. We must now consider the effects of frequency-independent colour-preferences on the significance of these findings. Consider the results obtained from the 1:1 populations of both experiments. Here, frequency-dependent effects should be absent and the values of the cross-product ratios:

$$\frac{bG}{gB} (= \frac{b}{g}) \quad \text{and} \quad \frac{yR}{rY} (= \frac{y}{r})^1,$$

should represent the relative preferences for the two colours used in each study. In 2a the values for b and g are not significantly different and $\frac{b}{g} = 1.076$. As can be predicted, when this figure is used in estimating the expected numbers taken from each population, the resulting curve scarcely differs from the straight line derived from assuming random predation (see Fig. 7).

In experiment 2b, however, $\frac{y}{r} = 0.62$.

The expected numbers taken, assuming this preference to be constant from population to population, are given in Table 7 and, as percentages, in Fig. 8. Three of the four relevant populations still show over-predation of the colours present at lower frequencies and these deviations are all highly significant. The overall tendency to take

¹Where G, B, R, Y and g, b, r, y represent the numbers of greens, browns, reds and yellows offered and taken respectively.

Figure 7

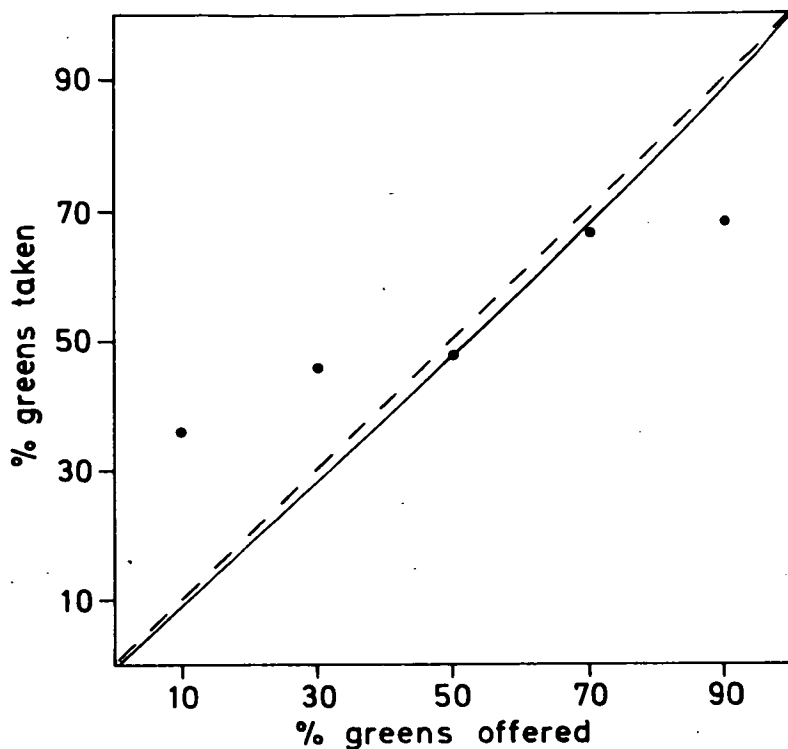
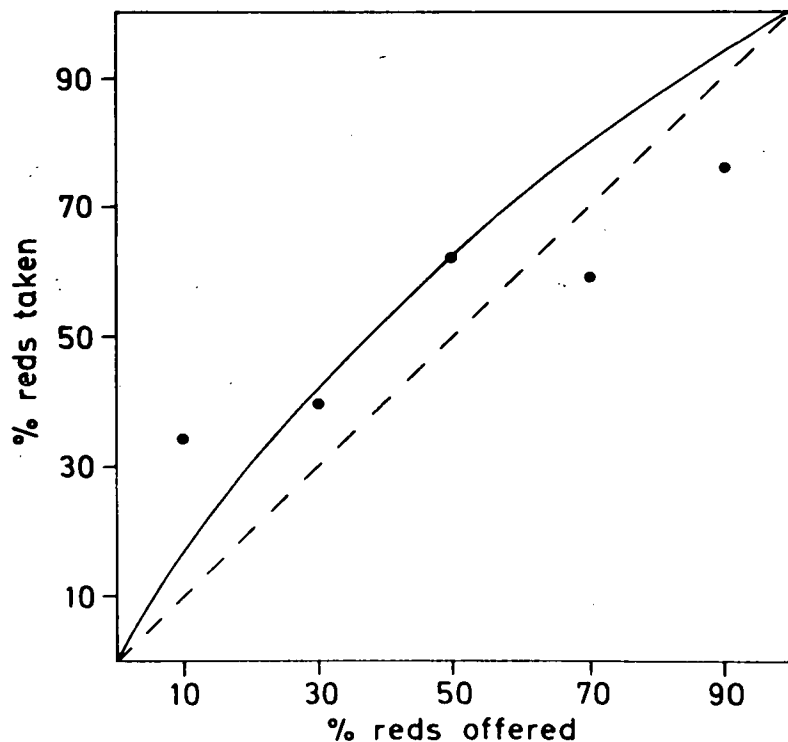


Figure 8



Figures 7 and 8

Experiment 2a (small greens, small browns) and 2b (small reds, small yellows) respectively: percentages of greens and reds taken against percentages offered. The straight (broken) lines indicate the expected relationships assuming random predation. The curves represent expected predation on the basis of the data from 1:1 populations.

the rarer colours is also still significant ($\frac{\Sigma X}{n} = 13.278$,
 $P < 0.001$).

4. DISCUSSION

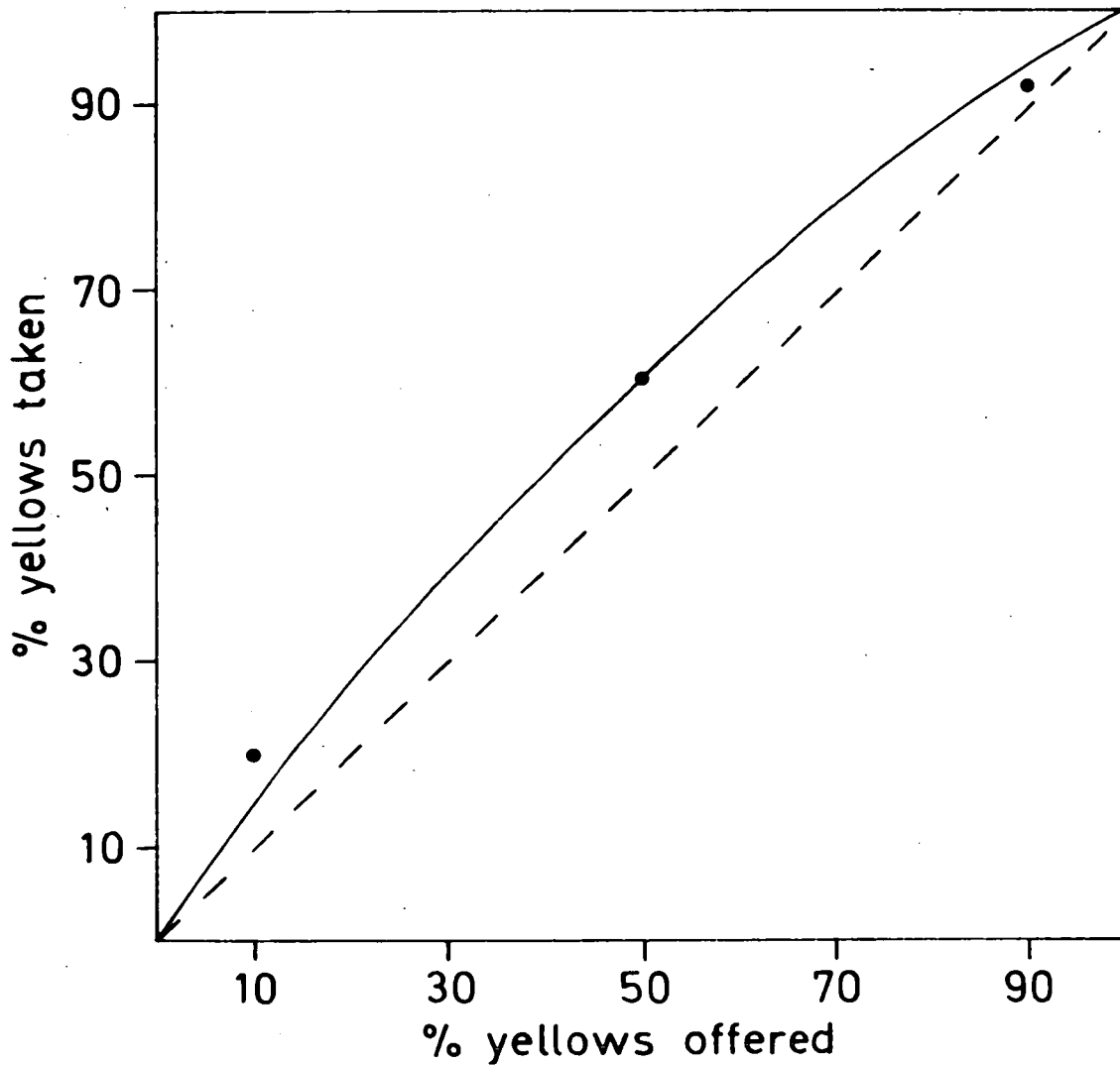
(a) Colour-preferences and searching images

The evidence obtained from predation on 1:1 populations does not suggest any large differences in the relative attractiveness of greens and browns (though red baits may have been preferred to yellows). At other frequencies the birds, overall, tended to take relatively too many greens. This implies that blackbirds, the main predators, favoured greens; a result that apparently contradicts information gained from other experiments (e.g. those described in Chapter VI) carried out with baits at lower densities.

Blackbirds tended to feed on only one colour during each visit (see experiments 1a, 1b and 1c). Though this suggests that they were using searching images, we cannot completely rule out the possibility that some or all of the birds were selecting on the basis of preferences extrinsic to the experiment. Pough (1964), in some experiments with individual chickadees, Parus atricapillus, obtained similar results. Birds in separate cages were presented with a series of thirty 1:1 choices between red and blue or yellow and white sunflower seeds. The prey were offered at densities of 100 per 18 inches-square. He found significant differences in the behaviour of the birds. As in the present experiments, each bird tended to pick out seeds of the same colour as its original choice.

Figure 9

Predation on yellow and red sunflower seeds: the relationship between the percentages of yellow seeds taken by chickadees and the percentages offered. The straight (broken) line is the expected relationship assuming random predation, whilst the curve represents expected percentages on the basis of data from 1:1 populations. (From Pough 1964).



(b) Selection of rare prey

The results imply that wild birds, on average, tend to select the colour offered in low frequency relatively more often than the common colour. This effect is opposite to that predicted by apostatic selection, as is well illustrated by comparing Figs. 7 and 8 with Figs. 3a and 3b. However, the theory of apostatic selection originally excluded very high densities (Clarke 1962a). For experiments specifically concerned with testing apostatic selection, the reader is referred to Chapter VI. The maintenance of polymorphism by such frequency-dependent selection depends on the assumption that predators, hunting in complex surroundings, encounter few numbers of prey at the same time. They should consequently acquire searching images that allow for greatest efficiency in exploiting the prey, and those prey-types that deviate from this image will be protected. Theoretically, these will be the rarest morphs. In the present experiments the predators could see a large number of prey individuals at the same time.

Comparable results have been obtained by other workers, notably Pough (1964). He offered dimorphic populations of painted sunflower seeds to groups of captive chickadees. The size of each population was 100 and the seeds were randomly distributed on 18-inch square trays. When groups of 6 birds were offered red and yellow seeds in ratios of 9:1, 1:9 and 1:1, they favoured yellows at all frequencies, but also tended to take the rare colours. Fig. 9 illustrates these results and can be compared directly with Figs. 7 and 8. Hayes (1962, quoted by Pough) obtained essentially similar results. Pough's original intention was to test for apostatic selection and he explained his apparently anomalous results by suggesting that the densities had been too high.

The present work with wild birds and Pough's, with chickadees, both support the general theory that when prey are dense predators tend to exert 'unifying' (Pielowski 1959, 1961) selection. In more general terms, unifying selection, where predators act to eliminate variability in a prey population, may be regarded as an example of selection whose effect has been described as 'stabilizing' (Schmalhausen 1949), 'centripetal' (Simpson 1953) and 'normalizing' (Waddington 1957). The behavioural cause of such an effect in a prey species is probably quite straightforward. In close groups of prey, any different or odd types are likely to be conspicuous, whether this difference is due to coloration, location or behaviour. To the human eye, and therefore presumably to the avian eye (Pumphrey 1961), the rare forms in my experiments appeared to stand out against the background of the rest. It is reasonable to conclude that the birds tended to take these types because they were relatively more conspicuous. This is in accordance with our knowledge that predators preferentially choose non-cryptic prey (see, e.g., Sumner 1934 and examples quoted by Cott 1940).

Such an overall trend was not the result of homogeneous responses by the birds. On each observed visit in experiments 1b and 1c, for example, blackbirds removed either only greens or only browns and, as already mentioned, this behaviour probably depended on which colour was taken first. We can hypothesise that for a given visit this first-eaten bait was most likely to be of the type that was rare and therefore conspicuous. Consequently, on average, this colour was taken relatively more often than the other.

Unifying selection can explain the remarkable uniformity of animals that live in close groups, for example in flocks of birds and

shoals of fish. The principle can also be used to predict that polymorphic species should exhibit least variation (in terms of the number of morphs) at very high densities. Polymorphic animals do, indeed, sometimes occur in high numbers per unit area. At Sanna Bay, Ardnamurchan, it is almost impossible to walk on the sand-dunes without treading on Copasa nemoralis and the density of Sphaeroma rugicauda in parts of the salt-marshes of the Tynninghame estuary, East Lothian, may be as great as 10 isopods per square inch (Dr.D.J. Heath, personal communication).

Owen (1963a, 1965a, 1965b) has studied the relation between density and the degree of polymorphism in populations of Linicolaria martensiana. He found that this snail was most polymorphic when it was commonest at densities of 100 per square metre. In absolute terms, this figure is comparable to the densities used by Pough. In effect, however, it is probably relatively lower. Consider the two environments. During the experiments with sunflower seeds and baits, all the prey were simultaneously exposed to the predators field of view. They were distributed in a two-dimensional, unobstructed plane. On the other hand, natural prey are distributed in many dimensions within complex surroundings. A predator searching for Linicolaria may, in fact, never encounter many snails at the same time, even if they are present in what to us seem like high densities. Indeed, such conditions may be more suited for apostatic selection. We will return (p.268ff) to the possible relationships between selection and density, after examining the results of experiments carried out at lower densities.

5. SUMMARY

In conclusion, the main results can be summarised as follows:

(a) Wild passerines, en masse, tend to select the rarer varieties of closely packed prey.

(b) This was probably an average result of heterogeneous responses by individual birds.

(c) The birds appeared to be hunting by searching image.

CHAPTER V CONDITIONING TO GREENS OR BROWNS

CHAPTER V CONDITIONING TO GREENS OR BROWNS

1. INTRODUCTION

The maintenance of colour-polymorphism by apostatic selection implies that predators can become conditioned to searching for one particular type of prey. In Chapter II it was pointed out that there is little direct evidence to suggest that wild predators behave in such a manner. This Chapter deals with attempts at conditioning wild birds to either green or brown baits.

2. PRELIMINARY EXPERIMENT

This early study has been described elsewhere (Allen 1967, Allen and Clarke 1968), but is included here for completeness.

(a) Procedures

The work was carried out in a garden near Dalkeith, Midlothian (O.S. grid reference: NT 352678). During six days in September, 1966, approximately 2,000 green baits were scattered on a background of dark soil marked out in a rectangular grid of forty one-metre squares. A population of forty greens and forty browns was then presented for three consecutive days. Blackbirds were the only predators.

After a lapse of one month, the familiarization was repeated with brown baits, after which the birds were again exposed to a population containing forty of each colour. During this period dunnocks, house sparrows and robins were feeding at the same time as blackbirds. It was, therefore, only practicable to observe the latter. Predation by 'small birds' was deduced from examining the baits at half-hour intervals.

Table 9

Preliminary experiment. Daily totals of baits taken after familiarization with one colour alone: soil background.

	Date	Hours of observation (BST)	Observed predation				“Small birds”	
			Blackbirds				(many)	
			(8 +)					
			G	B	G	B	G	B
Familiarized with greens	6.9.66	14.30–21.00	50 (9)	9 (1)	—	—	—	—
	7.9.66	11.15–19.00	111 (13)	14 (0)	—	—	—	—
	8.9.66	6.20–18.22	153 (32)	75 (8)	—	—	—	—
		Totals	314 (53)	98 (9)	—	—	—	—
Familiarized with browns	15.10.66	8.25–16.05	52 (8)	103 (20)	110	254		

(From Table 3, Allen & Clarke 1968)

(b) Results and discussion

The results are given in Table 9. After each training session the blackbirds took more of the familiar colour. The trend is highly significant despite heterogeneity between visits. This point is well made by the figures in parentheses in Table 9, which record the numbers of visits during which the specified colour was taken in excess. For each day the figures depart significantly in the expected direction from a 1:1 ratio.

After familiarization with greens there was a significant increase in the percentage of browns taken by blackbirds over every five visits ($P < 0.01$, Spearman's rank correlation test), suggesting that the birds were gradually recognising the browns as acceptable food. During the single day after familiarization with browns there was no corresponding increase in the number of greens taken by blackbirds, but the 'small birds' did show such a trend ($P < 0.01$).

3. REPEAT EXPERIMENTS

(a) Plan

Subsequent to the first, three series of analagous experiments were implemented. In outline, they were planned as follows:

Series 1 (Winter 1967) comprised four experiments at separate sites. At two of the locations, birds were trained on browns and, at the other two, on greens, before being presented with a 1:1 population.

Series 2 (Easter 1969) was identical with series 1, except that it consisted of six experiments.

Series 3 (Winter 1969) involved two experiments. In one, birds were fed on green baits before being given a 1:1 population (a).

Next, they were trained on browns and again offered a 1:1 population

(b). The second experiment was similar, except that browns were used in the first training session (a) and greens in the second (b).

(b) Materials and methods

(i) Locations

All the experiments took place on grass fields near Edinburgh. Their sites (nearest farms or villages) and O.S. grid references are given in Table 10.

The skewer-marked experimental plots were erected near the perimeter of each field, where nearby hedges or trees provided cover for potential predators. Each plot was a square consisting of twenty-five metre-squares.

(ii) Procedures

At each site, training was completed by scattering it with baits of one colour, every day for a week. Approximately 2,000 were consumed at each site. On the day following the end of familiarization, populations containing fifty of each colour were presented. These populations were randomly distributed and were maintained in the usual manner, by repeated replacement (see Chapter III). Table 11 gives the dates of the periods of familiarization and presentation of 1:1 populations. The experiments of series 1 and 2 each contained one day's presentation of a 1:1 population, whilst those in series 3 involved offering 1:1 populations for three days after each training session. With one exception, observations were made from a car. In experiment 12, the birds were watched in the open/^{from} beneath a hedge.

Table 10

Sites of experiments in series 1, 2 and 3, giving nearest farms or villages and O.S. grid references. All the experiments were carried out in fields in Midlothian, Scotland.

	BROWN-TRAINED	GREEN-TRAINED
	Expt. Site	Expt. Site
Series 1	1.1 Dryden Mains, Roslin. NT 275643 1.3 Capielaw, Rosewell. NT 302617	1.2 Broomhills, Burdiehouse. NT 268672 1.4 Dalhousie Chesters, Rosewell. NT 303637
Series 2	2.1 Liberton. NT 261702 2.3 Broomhills, Burdiehouse. NT 268673 2.5 Upper Dalhousie. NT 308635	2.2 Dryden Mains, Roslin. NT 274642 2.4 Hillend. NT. 255667 2.6 Thornton. NT 291610
Series 3	3.1a Capielaw, Rosewell. NT 302617 3.2b (as 3.2a)	3.1b (as 3.1a) 3.2a Liberton. NT 272704

Table 11

Dates of training and presentation of 1:1 populations in experiments of series 1, 2 and 3. All dates are inclusive.

	BROWN-TRAINED			GREEN-TRAINED		
	Expt.	Dates of training	Dates of presentation of 1:1 pops.	Expt.	Dates of training	Dates of presentation of 1:1 pops.
Series 1	1.1	12.11.67-18.11.67	19.11.67	1.2	18.11.67-19.11.67	20.11.67
	1.3	30.11.67-6.12.67	7.12.67	1.4	8.12.67-15.12.67	16.12.67
Series 2	2.1	5.3.68-10.3.68	11.3.68	2.2	4.3.68-10.3.68	12.3.68
	2.3	9.3.68-15.3.68	16.3.68	2.4	19.3.68-25.3.68	26.3.68
	2.5	19.3.68-24.3.68	25.3.68	2.6	24.3.68-30.3.68	31.3.68
Series 3	3.1a	20.11.69-27.11.69	28.11.69-30.11.69	3.1b	31.11.69-6.12.69	7.12.69-8.12.69
	3.2b	13.12.69-18.12.69	19.12.69-21.12.69	3.1a	3.12.69-9.12.69	10.12.69-12.12.69

Table 12

Numbers of baits taken from 1:1 populations by blackbirds and house sparrows (*) after training, and estimated numbers of birds involved (shown in parentheses).

	BROWN-TRAINED			GREEN-TRAINED		
	expt.	Numbers taken G B		expt.	Numbers taken G B	
Series 1	1.1	1 65 (2)		1.2	26 0 (2)	
	1.3	0 14 (1)		1.4	55 0 (2)	
Series 2	2.1	0 111 (4)		2.2	92 0 (2)	
	2.3	0 51 ₂ (4)		2.4	86 2 (2)	
		0 31 ₂ (6)				
	2.5	0 58 (2)		2.6	41 0 (2)	
Series 3	3.1a	0 71 (2)		3.1b	129 41 (2)	
	3.2b	24 135 (4)		3.2a	106 0 (4)	
Preliminary experiment		52 103 (8+)			314 98 (8+)	

(iii) Predators

Apart from one experiment, blackbirds were the only predators noted feeding. In experiment 2.3 house sparrows were also involved. The numbers of baits taken by these birds were estimated as in the preliminary experiment.

In each of the present studies, compared with the preliminary experiment, fewer individual blackbirds were involved. This was probably a result of the differences in environments; blackbirds are more abundant in gardens and woods than in open fields and hedgerows (Snow 1958). Estimates of the numbers of blackbirds participating in each experiment are given in Table 12.

(c) Results

Table 12 gives the numbers of greens and browns taken during the presentation of 1:1 populations. The data for each experiment in the first two series represent the results from a single day's presentation, whilst those of series 3 are grand totals of predation over three days. In addition to the results of series 1, 2 and 3, Table 12 gives the data from the preliminary experiment for easy reference.

In all, fourteen populations were presented to birds after separate training regimes. The effects of training are clear-cut. In each population, the familiar colour has been predated to excess. That is to say, during presentation of 1:1 populations, birds were continuing to search for, and eat, those baits that were the same colour as the ones on which they had been trained.

Table 13

Experiments 3.1 and 3.2 . Daily production
by blackbirds.

Experiment 3.1a			Experiment 3.1b		
BROWN-TRAINED			GREEN-TRAINED		
Date (1969)	Numbers taken		Date (1969)	Numbers taken	
	G	B		G	B
28 Nov	0	24	7 Dec	53	9
29 Nov	0	35	8 Dec	39	14
30 Nov	0	12	9 Dec	37	18
	0	71		129	41

Experiment 3.2b			Experiment 3.2a		
BROWN-TRAINED			GREEN-TRAINED		
Date (1969)	Numbers taken		Date (1969)	Numbers taken	
	G	B		G	B
10 Dec	5	56	19 Dec	35	0
11 Dec	6	36	20 Dec	44	0
12 Dec	13	43	21 Dec	27	0
	24	135		106	0

A further measure of the acquired preferences is given by the fact that in ten populations the unfamiliar colour was totally neglected, whilst in the remainder only one and two were taken (experiments 1.1 and 2.4 respectively). What is more, the unfamiliar colour was totally untouched in each of the three days of 1:1 presentation in experiments 3.1a and 3.2a, after the first training sessions. In other words, in twelve experiments there was a homogeneous response to the prey. It is legitimate, therefore, to compare statistically the observed and expected values of the proportions taken. The deviations from expected 1:1 selection are all highly statistically significant. Each has a probability of less than 0.001 that the result was due to chance alone.

The only experiments that revealed appreciable elimination of the uncountary varieties were 3.1b and 3.2b. Presentation of 1:1 populations after training in these studies had already been preceded by experiments 3.1a and 3.2a respectively. The birds were therefore familiar with both colours by the time the second training period was implemented. Yet by the time of the subsequent presentation of 1:1 populations, they were apparently again conditioned to searching for one particular colour, but now the varieties involved were the ones that had been 'unfamiliar' in the first experiment. They continued to take an excess of these colours on each of the three days of presentation in each experiment (Table 13). Nevertheless, in one experiment there was a significant increase in the proportions of the unfamiliar colour taken over every three visits, suggesting that the birds were re-learning to search for these prey ($r_s = 0.73$, $P < 0.05$, for experiment 3.1b; $r_s = 0.69$, not significant, for experiment 3.2b). In addition, there were significant differences in the proportions taken on the first and last days after the second training sessions, but not between any other

combinations of days ($\chi^2_{(1)} = 5.4447$, $P < 0.02$ for experiment 3.1b; $\chi^2_{(1)} = 5.0574$, $P < 0.05$ for experiment 3.2b).

The results for the two experiments of series 3 imply that preferences produced by a first session of familiarization can be changed by a second. Though it was difficult to identify reliably unringed individuals, there was no evidence for changes in the compositions of the predators after any of the training periods. It is therefore reasonable to assume that individual birds underwent changes of preference. This argument is strengthened by observations on a blackbird with two conspicuous white feathers in her tail. The numbers of baits taken by her in experiment 3.1 are shown in Table 14.

Table 14

Numbers of baits taken from 1:1 population by
a recognisable female blackbird in experiment 3.1

	Numbers Taken	
	G	B
After brown-training 28th Nov. - 30th Nov. inclusive	0	24
After green-training 7th Dec. - 9th Dec. inclusive	43	1

4. DISCUSSION

(a) Comparison between preliminary and repeat experiments

All the above experiments apparently demonstrate the striking effects of training. It will be noted, however, that the results of the duplicate experiments are more explicit than those of the preliminary study. This small discrepancy may be a function of the differences between the two types of environments: fields and hedgerows as opposed to gardens and woods. The former habitats support relatively fewer blackbirds (Snow 1958) and the numbers involved in the duplicate experiments were correspondingly lower. Probably as a consequence of their low densities, the compositions of blackbirds appeared to remain stable and confined to those with territories¹ in the immediate vicinities of the experiments. Thus each bird had a high chance of feeding on baits offered during training.

Gardens and woods, in contrast, support a higher density of blackbirds, and throughout the pilot experiment it seemed subjectively that new birds were periodically finding the experimental food supply. Consequently, some of the birds observed feeding on the 1:1 populations may have eaten few, or none, of the baits offered during training. This could explain why some birds took unfamiliar baits, sometimes even to excess.

(b) Effect of natural preferences

So far it has been assumed that green and brown baits are normally equally acceptable to birds. Hence the expected selection from the dimorphic populations was assumed to be 1:1. In fact,

¹The relevance of territory and territorial behaviour are discussed in Chapter VIII, in relation to some 9:1 experiments.

blackbirds generally seem to prefer browns (see Chapters VI, VIII) and this natural predilection could conceivably account for the results obtained after familiarisation with this colour. However, reference to experiments described in Chapter VI renders this possibility unlikely. The presentation of dimorphic populations, with browns nine times as common as greens, gave results for naive blackbirds (and one songthrush) on six separate occasions (see Table 20). The grand totals taken by these birds were 13 greens and 2602 browns, a ratio of approximately 1:200. In the brown-training experiments described above (neglecting the preliminary experiment and 3.2b, both of which involved an extra previous training session), 1 green and 370 browns were taken. That is to say, the proportions of browns and greens taken were almost twice as great in the present 1:1 experiments as in the specified 9:1 studies. Yet in the latter, browns were presented in relatively greater numbers. It is therefore reasonable to conclude that brown training does in fact reinforce any natural predilections for this colour.

(c) Conditioning

Summarising the main results, wild birds continued to search for familiar colours after each of sixteen separate training sessions. These conclusions will now be discussed with regard to the findings of other workers and, briefly, in the context of results reported elsewhere in this thesis.

The repeatability of these experiments is lent further weight by some similar work, using green and brown baits, done at Liverpool by Sister S. Shutt (personal communication). She fed blackbirds (no other birds were involved) on green lard-and-flour pellets for a week, on a background of red tiles. Twenty browns and twenty greens were

then presented at an unspecified density. Baits were not replaced when eaten and only a pair of birds were involved. On the first day, seventeen greens and only one brown were taken and on the next, only greens. On each of the succeeding two days the male blackbird was the first to visit the populations and took greens alone. Confronted with a scarcity of her preferred colour, the female was forced to commence eating browns.

Similar results for wild birds have been obtained by Oates and others (quoted by Cook 1971, pp.87-88). The prey were red and yellow 'maggots' made of flour, fat, and colouring and they were presented in populations of 49, at a density of one per square foot. Predators were housesparrows, blackbirds and starlings. After four days of training on one colour, both types were presented for four more days. Their proportions were either 90%, 70% or 50% of the conditioning colour. In ten out of twelve trials, a relative excess of the conditioned colour was taken (see Cook 1971, Table 4.1). As in my data, there was a suggestion that the tendency to remove the familiar colour declines with time.

It seems probable that the effect described in this Chapter is widespread in wild birds. Including myself, three authors (and probably others) have obtained similar results. Our data support Tinbergen's (1960) original contention that wild birds can build up searching images to prey and may consequently overlook new species, even if these are relatively common. Or, if the two prey were morphs of a species, then we have a mechanism capable of maintaining the polymorphism.

Further supporting evidence comes from experiments with captive birds. The work of Rabinowitch (1968) has already been described (p.36), but considered unsatisfactory since he used chicks of a very early age. Pough (1964), however, was able to demonstrate

the effects of conditioning on prey selection by captive chickadees. Birds were fed on either 100 yellow or 100 red sunflower seeds for two days before being presented with 70 of the familiar colour and 30 of the other. In other words, he offered 9:1 populations overall as in his other experiments (see Chapter IV, pp. 78-80) except that the birds were obliged to encounter 100 of the common sort before presentation of the remainder of the population. In comparison with his earlier experiments, he found that selection was now closer to expected, assuming random predation. Presumably, the tendency to take rarer forms was being balanced by a conditioned preference for the commoner type. More recently, similar results have been obtained by Mrs. Pat Miller (personal communication) for quails feeding on red and blue pastry prey.

Other results comparable to mine have been found for fish (Reighard 1908, Beukema 1968, Smith 1967) and mammals (Soane 1970). Most of them (and also those with birds) involved morphs that are visibly very distinct. Green and brown baits are no exceptions to this rule. The morphs of many species are often similar in colour. Croze (1967, 1970) is the only worker to have used visually similar artificial morphs and his findings will be discussed later, in conjunction with experiments of my own. The evidence presented in that section (Chapter IX) will lend more weight to the present findings.

More support is derived from some of the findings described in the next Chapter, which deals with the responses of untrained birds when confronted with populations containing greens and browns in the proportions of nine to one or one to nine.

5. SUMMARY

In conclusion, we can summarise the main results as follows:

- (a) In 8 experiments, wild birds were trained to search for green or brown baits.
- (b) When presented with a mixture of both in equal proportions they took the familiar colour to excess. This occurred in all experiments.
- (c) In 3 experiments it was possible to reverse the preference by carrying out a second period of training.
- (d) The results of the same 3 experiments indicated that the effect of conditioning gradually lessened with time.

CHAPTER VI 9:1 EXPERIMENTS: PREDATION BY GROUPS OF BIRDS

CHAPTER VI 9:1 EXPERIMENTS: PREDATION BY GROUPS OF BIRDS

1. INTRODUCTION

This section deals with attempts to determine whether groups¹ of naive birds will preferentially search for the commoner colours in populations of green and brown baits. The background to this line of enquiry has been discussed in Chapter II (pages 41 - 47).

At first it was decided to present the baits in populations with one colour nine times as common as the other and later experiments adhered to these proportions. Each experiment consisted of two parts. Birds were first presented with populations having one of the colours nine times as common as the other. After a few days they were offered control populations with the other colour as the common variety. Such a design meant that two basic types of experiments were carried out; they started with populations of either 9 greens: 1 brown, or 1 green: 9 browns.

2. PRELIMINARY EXPERIMENTS

Two of these studies were carried out as part of a B.Sc. Honours project (Allen 1967). The results of the first experiment have since been further analysed and have been published (Allen and Clarke 1968).

(a) Experiment 1: presentation of 9G:1B populations followed by 1G:9B populations

(i) Materials and methods

A 10m X 10m grid was laid on the lawn outside the Department of

¹This does not necessarily imply that the birds were feeding in the same place at the same time.

Table 15. Experiment 1. Daily totals of baits taken:
grass background.

180 greens : 20 browns									
Date	Hours of observation (BST)	Blackbirds (6 +)		Observed predation				H. Sparrows	
		G	B	Starlings (2)		Dun- nocks (2)		(many)	
		G	B	G	B	G	B	G	B
30.7.66	9.03-12.00	2	0	—	—	—	—	—	—
1.8.66	10.30-18.15	61	9	0	1	1	0	—	—
2.8.66	8.30-16.30	71	22	—	—	4	0	—	—
3.8.66	9.20-15.15	71	17	—	—	5	0	10	1
5.8.66	10.30-17.05	45	11	—	—	14	0	86	2
6.8.66	5.09- 7.51	69	15	—	—	—	—	14	0
7.8.66	16.06-18.10	35	12	20	2	—	—	57	0
Grand totals		354	86	20	3	24	0	167	3
Expected 9 : 1		396.0	44.0	20.7	2.3	21.6	2.4	153.0	17.0
Expected, constant selection		349.0	91.0	15.2	7.8	23.4	0.6	154.4	15.6

Experiment 2									
20 greens : 180 browns									
Date	Hours of observation (BST)	Blackbirds		Observed predation					
		(2 +)		Starlings (many)		Dun- nocks (2)		H. sparrows (many)	
		G	B	G	B	G	B	G	B
9.8.66	9.30-15.15	—	—	0	7	0	1	15	42
10.8.66	10.30-17.30	0	5	—	—	—	—	5	155
11.8.66	10.50-16.10	0	14	1	37	—	—	14	183
14.8.66	15.05-18.10	0	13	0	45	0	2	4	136
15.8.66	11.40-14.10	0	13	0	44	—	—	2	60
17.8.66	14.30-18.35	1	11	1	19	—	—	9	74
18.8.66	10.25-17.40	0	24	1	36	1	4	29	111
Grand totals		1	80	3	188	1	7	78	761
Expected 1 : 9		8.1	72.9	19.1	168.9	0.8	7.2	83.9	755.1
Expected, constant selection*		3.7	77.3	4.5	186.5	2.8	5.2	91.4	747.6

* See text.

The approximate numbers of birds involved in each experiment are given at the heads of the columns.

(Based on Table 1, Allon and Clarke 1968)

Zoology, University of Edinburgh. Within the grid, 180 green and 20 brown baits were distributed at random, two baits per metre square. Observations were made from a first-floor window and the population was maintained in the usual manner. During the experiment the grid was under continuous observation and a record was kept of the numbers of baits taken by the birds at each visit. After seven days of predation, the experiment was repeated with a population of 20 greens and 180 browns.

(ii) Results and discussion

The daily totals of baits eaten are shown in Table 15. Below the grand totals are given the expected numbers based on the assumption that there is no selection. The blackbirds and starlings took more browns than expected in both experiments. Dunnocks and sparrows, on the other hand, took more greens in the first experiment and more browns in the second. It is clear, therefore, that the birds did exercise visual selection and the direction of selection could change within a few days. These changes did not seem to be caused by alterations in the colour of the background, which remained apparently constant throughout the period of study.

It remains to enquire whether the differences between the two experiments are related to the frequencies of the colours. On the basis of the grand totals we can calculate for each species the expected numbers of prey eaten, assuming that the selection remained constant throughout the period of study. If this were so the cross-product ratio:

$$\frac{\text{No. of greens offered} \times \text{No. of browns eaten}}{\text{No. of browns offered} \times \text{No. of greens eaten}}$$

should be the same in both parts of the experiment.

Table 16. Experiment 1. Numbers of baits taken by blackbirds during individual visits on August 2, 1966.

Visit	No. of baits taken	
	G	B
1	4	0
2	7	0
3	3	0
4	3	0
5	9	0
6	5	0
7	5	0
8	2	0
9	0	10
10	24	0
11	3	0
12	5	0
13	1	0
14	0	12
Total	71	22

(From Table 2, Allon and Clarke 1968)

The expected numbers based on assuming constant selection in both experiments, are given in the second row below the grand totals. It can be seen that, in fact, all four species took a larger number of common forms than expected and a smaller number of rare ones. Thus the birds appeared to select in a frequency-dependent manner. Direct comparison of observed and expected numbers suggests that the effect is highly significant $\left(\frac{(\sum X)^2}{n} = 20.19, P < 0.0001 \right)$. This comparison, however, is not strictly legitimate because of heterogeneity within the series, deriving from two sources:

Heterogeneity between days. For example, in the second part, house sparrows took the two colours in different proportions on different days $(\chi^2_{(6)} = 59.15, P < 0.001)$.

Heterogeneity between visits. Even where there is no significant heterogeneity between days, as with the results for blackbirds, there is strong evidence that the proportions differed from visit to visit. Table 16 shows the numbers of green and brown baits taken by blackbirds on August 2nd, 1966. Each visit by an individual bird is recorded separately. The data are not amenable to analysis by chi-squared, but it is clear that they are very significantly heterogeneous. If the birds were taking the baits at random, but encountering them in the proportions of seventy-one greens to twenty-two browns, then the probability of a bird taking twelve browns in succession (as on visit 14) would be less than 1 in 10^7 .

When this heterogeneity is taken into account, the frequency-dependent effects, although striking, cannot be regarded as formally significant.

Table 17 Experiment 2.1. Daily totals of baits taken

Predators - two blackbirds, one songthrush
Background - grass

a. 20 greens: 180 browns

Date (1967)	Hours of observation (G.M.T.)	Observed predation	
		G	B
18.1	7.48 - 16.30	1	58
19.1	7.50 - 16.51	0	49
20.1	7.40 - 17.00	0	38
21.1	8.25 - 17.00	0	54
22.1	7.35 - 17.00	0	58
23.1	8.20 - 17.00	0	55
	Grand totals	1	312
		(1.1)	(311.9)

b. 180 greens: 20 browns

Date (1967)	Hours of observation (G.M.T.)	Observed predation	
		G	B
24.1	8.35 - 17.00	6	39
25.1	8.10 - 17.00	18	40
26.1	8.07 - 17.00	17	37
27.1	8.14 - 17.00	5	33
28.1	8.15 - 17.00	9	45
29.1	9.00 - 17.00	12	36
30.1	8.30 - 17.00	16	50
31.1	7.50 - 17.15	9	47
	Grand totals	92	327
		(91.5)	(327.5)

(Numbers in parentheses represent the grand totals expected on the assumption of constant selection).

(b) Experiment 2.1¹: presentation of 1G:9B populations followed by 9G:1B populations

(i) Materials and methods

The predators involved in both parts of this experiment were two blackbirds and a thrush. All were colour-ringed and results were obtained for predation by each one. Here we shall consider their combined predation, whilst their individual responses will be examined in Chapter VII.

The procedures are described fully in the next Chapter. Summarising them, on 16th January 1967 a 10m X 10m grid was laid down on a lawn at my Reading home. For six days the birds were presented with populations containing 20 greens and 180 browns. They were then offered 180 greens and 20 browns for a further 8 days. Other populations were then presented but these do not concern us here (see p.151). All the populations were continuously observed and they were all presented during most of the daylight hours (see Table 17).

(ii) Results and discussion

Table 17 gives the pooled daily results for predation by the three Turdidae. Too many browns were clearly taken from the two types of population. If this preference is assumed to be frequency-independent and constant in both parts of the study we can derive the expected values shown in parentheses. The magnitudes of the deviations are clearly negligible.

The birds searched mainly for browns after the relative composition of the baits was changed. These daily results were not significantly

¹Experiments 2.2 and 2.3 are described in Chapter VIII.

Table 18 Experiment 4. Daily totals of baits taken

		Date	Hours of observation (G.M.T.)	Blackbirds (2-4)		Dunnocks (2)		Robins (2)		Blue Tits (2)		H.sparrows (many)	
				G	B	G	B	G	B	G	B	G	B
a. 20 greens: 180 browns	2.12	12.15 - 16.20	0	21	-	-	1	2	-	-	-	-	
	3.12	9.15 - 16.30	0	26	-	-	1	4	-	-	4	23	
	4.12	9.15 - 16.45	0	35	0	4	-	-	-	-	16	80	
	5.12	9.25 - 16.30	0	29	0	2	0	4	0	8	13	81	
	6.12	9.35 - 16.30	0	67	1	15	0	5	0	7	3	59	
	7.12	9.41 - 16.20	0	54	0	13	0	6	0	11	11	53	
	Grand totals		0	232	1	34	2	21	0	26	47	296	
Expected, 1:9		23.2	208.8	3.5	31.55	2.3	20.7	2.6	23.4	34.3	308.7		
Expected, constant selection		3.3	228.7	1.4	33.6	2.2	20.1	0.3	25.7	50.3	293.7		
b. 100 greens: 100 browns	9.12	9.35 - 16.25	16	50	1	2	3	1	1	5	10	38	
	10.12	9.40 - 16.50	11	47	4	5	0	3	1	2	25	20	
	11.12	9.20 - 16.50	12	49	7	9	0	2	1	2	16	11	
	12.12	9.15 - 16.40	7	48	7	9	1	5	2	0	29	53	
	Grand totals		46	194	19	25	4	11	5	9	80	122	
Expected, 1:1		120.0	120.0	22.0	22.0	7.5	7.5	7.0	7.0	101.0	101.0		
Expected, constant selection		27.7	212.4	12.0	32.0	7.2	7.8	1.1	12.9	121.4	80.6		
c. 180 greens: 20 browns	13.12	9.40 - 16.55	32	20	15	5	4	0	3	1	68	6	
	14.12	9.20 - 15.30	44	33	14	6	2	1	-	-	40	3	
	15.12	9.37 - 16.10	41	21	12	0	4	0	-	-	37	0	
	Grand totals		117	74	41	11	10	1	3	1	145	9	
Expected, 9:1		171.9	19.1	46.8	5.2	9.9	0.1	3.6	0.4	138.6	15.4		
Expected, constant selection		103.1	87.9	40.2	11.8	9.8	1.2	1.7	2.3	143.4	10.6		

heterogeneous ($\chi^2_{(5)} = 4.30, P > 0.50$) despite variation of the individual responses. Two birds searched for browns almost exclusively when rare, but the other relaxed its preference on the first day after changeover. We shall return to these birds in the next Chapter.

(c) Experiment 4: presentation of 1G:9B populations followed by 1G:1B and 9G:1B populations

This experiment, carried out in the late winter of 1968, was essentially a repeat of experiment 2.1, except that 1:1 populations were offered between the 1:9 and 9:1 populations.

(i) Materials and methods

On 2nd December 1968 a grid of 100 metre-squares was laid down on the lawn of a garden in Dalkeith. For seven days birds were presented with 20 greens and 180 browns. After a lapse of one day, equal numbers of greens and browns were offered for four days, followed by three days of 180 greens and 20 browns.

The baits when presented were observed continuously; blackbirds and house sparrows were the main predators but robins, dunnocks and blue tits were also involved in all three parts of the study. In addition, later populations were visited by great tits (Parus major L.), coal tits (P. ater L.) and starlings.

(ii) Results and discussion

Table 18 shows the daily totals of baits taken. The only results that reveal significant heterogeneity in the proportions taken per day are those for house sparrows in part b. ($\chi^2_{(3)} = 16.83, P < 0.001$). As in experiment 1, however, the blackbirds exhibited considerable variation in the proportions taken per visit when feeding on populations presented during b. and c.

Below the grand totals are given the expected numbers based on random predation. The birds were clearly discriminating between the baits; thus the blackbirds, dunnocks, robins and blue tits took more browns than expected in all three parts. The house sparrows took too many greens in a. and c. and too many browns in b.

The Table also gives the expected predation based on the assumption that selection was constant in a. and c. These values were derived in the same manner as before (see page 104). In all ten cases the commoner colour was taken more often than expected. Overall this effect is statistically significant $\left(\frac{(\sum X)^2}{n} = 5.74, P < 0.02 \right)$.

The data from the 1:1 populations need some comment. In every case browns were taken to excess on the basis of 1:1 ratios, suggesting that the birds carried-over preferences learned from part (a) of the experiment. Overall this effect is statistically highly significant $\left(\frac{(\sum X)^2}{n} = 53.07, P < 0.001 \right)$. On the basis of constant selection in parts (a) and (b) we find that robins and house sparrows took more browns than expected $(\chi^2_{(1)} = 2.803, P > 0.05, \text{ not significant}; \chi^2_{(1)} = 35.39, P < 0.001)$. On the other hand the blackbirds and dunnocks for some reason took more greens than expected $(\chi^2_{(1)} = 13.76, P < 0.001; \chi^2_{(1)} = 5.429, P < 0.02)$. The overall selection was not significantly different from the expectation assuming constant selection $\left(\frac{(\sum X)^2}{n} = 0.628, P < 0.8 \right)$.

3. REPEAT EXPERIMENTS

Two of the three continuously observed experiments apparently showed statistically significant frequency-dependent selection. However, all the studies revealed considerable heterogeneity in their results and it must be re-emphasised that the use of chi-squared was

therefore not strictly legitimate. This problem could be overcome, to some extent, by seeing whether repeat experiments give similar evidence for apostatic selection. Consequently, eleven more experiments were carried out: six followed the design of experiment 1 and five were similar to experiment 2. During these experiments the birds were not always observed.

(a) Plan of Work

The experiments were grouped into four separate series carried out in 1968 and 1969. These series were designed as follows.

(i) Series 3 - August 1968

Four experiments were involved; two were carried out on grass and two on soil. All were at sites within the City of Edinburgh and were less than one mile from the Department of Zoology. The populations were not always observed continuously: occasionally they were left unattended and re-examined on return. Birds could therefore be fed at more than one site on the same day. Each period of predation, observed or unobserved, constituted a 'trial'.

The populations contained 100 baits laid out in 5m x 5m grids. Ideally they should have been visited as frequently as possible and it was hoped to keep the recorded predation to below 50%. This was not always possible, because of a combination of high rates of predation and transport difficulties. Larger populations may have helped but were considered impractical (but see series 5 and 6).

(ii) Series 5 - February to April 1969

The six experiments of this series were similar in basic design to those of series 3. However, all were carried out on fields in Midlothian and they involved populations of 200 baits distributed in 10m x 10m grids. These larger populations and the use of a car for

getting from site to site ensured that predation could be kept to within reasonable limits.

The start of the series was delayed by heavy falls of snow during the first two weeks of February. During the middle of the month, the sites were almost clear of snow and the first experiments started on the 14th. On the same day more snow fell and the plots remained completely covered until the end of the month. A gradual thaw set in at the beginning of March and all the sites were completely clear by the 5th.

(iii) Series 6 - May to June 1969

This set contained 2 experiments carried out in grass fields. The populations were distributed in 10m x 10m grids and, like those of the experiments in the other series, were not under continuous observation.

Rain fell on various occasions and was particularly heavy on 6th and 14th May and on 21st and 22nd June.

(b) Experiments and results

These experiments were studies unto themselves and, like the first three, demand individual attention. However it is felt that the insertion of these bulky results in the ensuing pages would interrupt the present theme. The reader should therefore refer to Appendix A, pages 123 to 145 for full details of the eleven repeat experiments.

4. SUMMARY OF DATA

Tables 19 and 20 summarise the data. They give the grand totals of baits taken from the two types of populations presented in all the experiments described in this Chapter. Data for predation on 9G:1B

Table 19

Grand totals of baits taken in 9:1 experiments with 9G:1B populations followed by 1G:9B populations. Predators: blackbirds (Bl), songthrush (So), house sparrows (HS), dunnecks (D), starlings (St).

9G : 1B $\longrightarrow$ 1G : 9B								
Expt.	Pred.	G	B	G	B	CPR	$\chi^2_{(1)}$	P
1	HS	167 (154.4)	3 (15.6)	78 (91.4)	761 (747.6)	0.907	$\left. \begin{array}{c} 20.19 \\ \left(\frac{\sum X^2}{n} \right) \end{array} \right\}$	<0.001
	D	24 (23.4)	0 (0.6)	1 (2.8)	7 (5.2)	0.21		
	St	20 (15.2)	3 (7.8)	3 (4.5)	188 (186.5)	4.89		
	Bl	354 (348.9)	86 (91.1)	1 (3.7)	80 (77.9)	2.41		
3.1	Bl, So, HS	363 (349.1)	120 (133.9)	1 (6.3)	202 (196.7)	3.46	6.63	<0.02
3.4	Bl, St, HS	128 (112.5)	47 (62.5)	1 (5.7)	262 (257.3)	5.00	9.00	<0.01
5.2	Bl	353 (343.0)	56 (66.0)	11 (17.4)	278 (271.6)	1.73	4.32	<0.05
5.3	Bl	231 (217.0)	40 (54.0)	7 (14.5)	299 (291.5)	2.24	8.60	<0.01
5.4	Bl	192 (175.6)	39 (55.4)	6 (13.6)	348 (340.4)	2.84	10.82	<0.01
6.2	Bl	619 (601.3)	148 (165.7)	5 (13.6)	313 (304.4)	2.48	8.13	<0.01

Table 20

Grand totals of baits taken in 9:1 experiments with 1G:9B populations followed by 9G:1B populations. Predators: blackbirds (B1), songthrush (So), house sparrows (HS), dunnecks (D), robins (R).

1G : 9B $\longrightarrow$ 9G : 1B								
Expt.	Pred.	G	B	G	B	CPR	$\chi^2_{(1)}$	P
2.1	B1, So	1 (1.1)	312 (311.9)	92 (91.5)	327 (327.5)	32.23	0.01	not sign.
4	HS	47 (51.3)	296 (293.7)	145 (133.4)	9 (10.6)	0.664	$5.74 \left(\frac{(\sum X)^2}{n} \right)$	<0.02
	D	1 (1.4)	34 (33.6)	41 (40.2)	11 (11.8)	2.66		
	R	2 (2.2)	21 (20.1)	10 (9.8)	1 (1.2)	1.07		
	B1	0 (3.3)	232 (228.7)	117 (103.1)	74 (87.9)	7.68		
3.2	B1	2 (4.0)	734 (732.0)	63 (50.5)	102 (114.5)	20.40	5.44	<0.02
3.3	B1, St, HS	2 (5.8)	287 (283.2)	167 (159.1)	139 (146.9)	8.31	3.35	not sign.
5.1	B1	3 (13.5)	368 (357.5)	372 (348.0)	90 (114.0)	2.95	15.18	<0.001
5.5	B1	3 (14.2)	350 (338.8)	380 (356.1)	81 (104.9)	2.65	16.25	<0.001
6.1	B1	4 (16.5)	606 (593.5)	411 (375.4)	131 (166.6)	3.99	20.72	<0.001

populations followed by 1G:9B populations are shown in Table 19, whilst Table 20 presents the results from the complementary types of experiments. Where possible (i.e. in expts. 1 and 4) predation by different species is shown separately. This means that the Tables show 20 sets of data from 14 experiments¹.

Cross-product ratios were derived by assuming that selection was constant in both parts of the experiments and are shown in the Tables. The numbers in parentheses represent the expected predation and were calculated on the basis of the cross-product ratios. Also shown are the values of chi-squared for the deviations of observed from expected predation and the probabilities of these deviations being due to chance alone.

5. DISCUSSION

The discussion naturally centres on the evidence for apostatic selection. We also examine the frequency-independent colour preferences and discuss the direct evidence suggesting that the birds can become conditioned to searching for familiar colours.

(a) Apostatic selection

Reference to Tables 19 and 20 will reveal that most of the grand totals deviate from expected in the directions predicted by apostatic selection. Of the 20 sets of data, 19 exhibit over-predation of the common colours and under-predation of the rare ones, in both parts of the experiments. This proportion of scores is highly significant ($P < \frac{0.001}{\text{binomial test}}$) and overcomes the problem of heterogeneity within sets.

¹The data for blackbirds have now been published (Allon 1972).

In terms of experiments, 12 out of 14 revealed statistically significant deviations from expected predation assuming constant selection. As can be seen from Table 19, there was apparently significant frequency-dependent selection in all 7 experiments of the type 9G:1B $\rightarrow$ 1G:9B. The findings of experiment 1 therefore seem to be repeatable. When populations were presented in the reverse sequence (see Table 20), the results of 5 of the 7 experiments exhibited significant apostatic selection. The duplicate experiments did not reveal the existence of such strong brown preferences as were apparent in experiment 2.1, but the tendency was sometimes present (see below).

The experiments encompassed a variety of experimental conditions. Some took place in winter; on short grass (2.1), or against a background of snow (parts of 5.1, 5.2 and 5.3). Under the latter conditions we might expect selection to be close to random (see p. 118). Other studies were carried out in spring (5.4, 5.5), and summer (all of series 3 and 6). The experimental areas had various backgrounds; soil (3.2, 3.4), short uniform grass (1, 2.1, 3.1, 3.2, 4, 5.5, 6.2) or longer patchy grass (5.1, 5.2, 5.3, 5.4, 6.1). Different birds were involved at different sites.

There was also heterogeneity within experiments. Besides preliminary experiment 1, only experiments 5.2 and 5.4 did not show significant heterogeneity of the proportions of greens and browns taken per trial when birds were feeding on 9G:1B populations.

Yet the overall results are remarkably alike, despite the dissimilarities of the experimental conditions. There was always (with the exception of 2.1) a tendency for the common colour to be taken more often than expected on the basis of constant selection. The experiments therefore appear to be consistently repeatable.

(b) Colour preferences

The preliminary experiments took place on lawns. In experiment 1 the Turdidae tended to take too many browns from both types of population, assuming 9:1 expectations, and this observation was supported to even greater effect by the second experiment. Subsequent experiments (3.1, 3.2, 4, 5.4, 5.5, 6.1, 6.2) on grass backgrounds also gave similar results for blackbirds and thrushes. During the presentation of 10 greens and 90 browns in experiment 3.2, for example, the browns were completely eliminated during 4 of the 10 trials, whilst apart for the loss of one bait, the greens were untouched. The average cross-product ratios derived from the grand totals of the results of these experiments are shown in the relevant Tables: all are greater than unity.

An explanation for the preferences of the Turdidae could be that the browns were less cryptic than greens against grass. To the human eye, however, this did not appear to be the case. What is more, the results of other experiments indicate that brown preferences are independent of the colour of the background.

Snow covered the ground during many of the trials of experiments 5.1, 5.2 and 5.3. In comparison with grass, this surface was more uniform with regard to both colour and composition. Against it greens and browns appeared to be equally highly conspicuous. If the colour preferences were a function of the background coloration we might expect relatively fewer browns to have been taken in these experiments than in those on grass. Another factor might also be expected to contribute to making selection random. Various workers (Young 1948, Prop 1960, Boukema 1968) have shown that predators appear to relax their food-preferences when hungry, as when their normal environments

are covered by snow. References to the results of the three experiments (pp. 140 - 141, pp. 128 - 129, pp. 130 - 131) shows that the Turdidae still took more browns than expected on the basis of the proportions offered.

Populations presented on soil (experiments 3.3 and 3.4) produced results comparable to those just discussed, but for the combined predation by a mixture of different species. Though greens appeared more conspicuous, too many browns were taken from both types of population than expected by assuming random selection. This preference was so pronounced on two days in 3.3 that all the common browns were taken whilst the greens were left unharmed¹ (see Table 29, p. 138). It will be noticed that these findings emulate those of 3.2, an experiment carried out on a grass background.

Large numbers of birds were feeding during 3.3 and 3.4 and it was impossible to obtain data for separate species. Yet their responses were probably relatively homogeneous. This is particularly noticeable in the case of 16:9B populations; as shown by Table 29 and Table 23, all the birds were almost completely restricted to removing browns. It follows that the house sparrows, for example, must have had preferences for browns in the two experiments. This is contrary to other results (experiments 1 and 3) where it was noted that house sparrows favoured greens. A possible reason for this discrepancy and for the uniformity of the inter-species predilections is given by the observation that the birds had been seen feeding on, or in, piles of brownish hep manure near the experimental plots (see p. 139 and p. 127). If we accept the searching image a priori then the birds may be expected to have become conditioned to searching for brown prey.

¹Incidentally these results directly contradict a statement by Croze (1967, p. 139) that 'a green mutant, regardless of its low frequency, could not hide from predators on a homogeneous brown background'.

Table 21

Numbers and percentages of baits taken on first days of predation on 9G:1B populations by blackbirds (B1) alone and by blackbirds plus other birds (So = songthrushes, HS = house sparrows, St = starlings)

(a) In experiments where 9G:1B populations were presented first.

expt.	birds	G	B	%B
1 ^a	B1	63	9	12.5
3.1	B1,So,HS	45	19	29.7
3.4	B1,St,HS	52	10	12.9
5.2	B1	31	6	16.2
5.3	B1	14	8	36.4
5.4	B1	12	4	25.0
6.2	B1	5	7	58.3

(b) In experiments where 9G:1B populations were presented second.

expt.	birds	G	B	%B
2.1	B1,So	6	39	86.6
3.2	B1	1	42	97.7
3.3	B1,St,HS	29	17	36.9
4	B1	32	20	38.5
5.1	B1	28	18	39.1
5.5	B1	20	39	66.1
6.1	B1	84	54	39.1

^a Data are the total predation for the first 2 days

(c) Conditioning

When these colour-preferences were taken into account by assuming that they were independent of the relative frequencies of the baits offered, we found that, on average, selection was apparently apostatic in each experiment. This implies that the birds tended to hunt by searching images. Is there any direct evidence to support this assumption?

Attention is focused on predation by Turdidae, alone and with other birds, after the change of populations in the 1G:9B $\rightarrow$ 9G:1B experiments. The second preliminary experiment showed that preferences for browns can be strong even when these colours are rare. None of the repeat experiments produced such marked responses, though in 3.2 the results of the first two days after changeover disclosed almost 100% predation of browns (see Table 28, p. 136). In the remaining experiments the proportions of browns taken after changeover were generally highest during the first day.

This initial overpredation of rare browns could possibly be due to natural preferences extrinsic to the experiments. If this were the case, we would expect similar selection to occur at the beginnings of the 9G:1B $\rightarrow$ 1G:9B experiments. Table 21 compares the results from experiments where these populations were (a) and were not (b) preceded by 1G:9B populations. The proportions taken in the former situation tend to be higher than the values in the other set of data. This suggests that the birds had 'carried-over' preferences obtained during exposure to 1G:9B populations. In other words, their natural brown preferences had been strengthened: they were hunting by searching image.

6. SUMMARY

In 14 experiments wild passerines en masse were presented with populations containing one colour nine times as common as the other. To summarise, the main conclusions were as follows:

- (a) A preliminary experiment revealed considerable heterogeneity in the data and it was therefore necessary to carry out repeat studies.
- (b) Blackbirds took more browns than expected on the basis of 9:1 ratios.
- (c) In 13 out of 14 experiments the deviations from the expected, based on the assumption of constant selection, were in the direction predicted by apostatic selection.
- (d) Taking into account the results for separate species, 19 out of a total of 20 sets of data gave evidence of apostatic selection.
- (e) There is evidence that the birds were hunting by searching image.

APPENDIX A: TABLES 22-32

Trial-by-trial results for 9:1 repeat experiments of Chapter VI

(a) Key to Tables

The Tables give the following details of each experiment:

1. Species of predator and estimated number of each
(in parentheses).
2. Type of background.
3. Composition of populations.
4. Dates and times of trials.
5. Numbers of greens and browns taken per trial.
6. Grand totals of greens and browns taken from the two
types of population.
7. Expected grand totals, calculated on the basis of
constant selection (in parentheses, below observed grand totals).
8. Asterisks indicate unobserved trials.
9. 's' indicates that over 50% of the area of the plot was
covered by snow during the relevant trial.

(b) Tables and experiments/see overleaf

Table 22 Experiment 3.1. Totals of baits taken during trials

Predators - blackbirds (8), songthrush (1), housesparrows (1-4),
Background - grass

a. 90 greens:10 browns

Date (1968)	Times (B.S.T.)	Predation		
		G	B	
1.8	12.15 - 17.00	30	9	*
	17.15 - 20.00	15	10	*
2.8	9.10 - 10.15	8	10	*
	10.20 - 14.30	18	10	*
	14.45 - 16.30	14	9	*
	16.52 - 20.31	5	10	*
3.8	9.02 - 11.05	73	8	*
	11.31 - 17.05	37	2	*
5.8	10.45 - 11.50	1	1	
	11.50 - 17.00	42	10	*
	17.20 - 19.20	9	7	
7.8	9.25 - 11.10	16	1	
	11.50 - 15.00	28	8	*
	15.28 - 16.35	8	5	
	16.41 - 18.10	33	6	*
8.8	10.00 - 14.50	21	14	
12.8	10.30 - 12.00	5	0	
	Grand totals	363	120	
		(349.1)	(133.9)	

b. 10 greens:90 browns

Date (1968)	Times (B.S.T.)	Predation		
		G	B	
13.8	11.39 - 12.33	1	19	
	12.40 - 15.45	0	44	*
	16.03 - 19.41	0	42	*
14.8	20.10(13.8) - 9.01	0	79	*
	9.20 - 14.01	0	18	*
	Grand totals	1	202	
		(6.3)	(196.7)	

(1) Presentation of 9G:1B populations followed by
1G:9B populations

Experiment 3.1

Method The grid was laid down on a lawn of Abden House, Newington, Edinburgh (O.S. grid reference NT 269724) and populations were presented on the dates shown in Table 22. Observed trials revealed that predation was mainly due to blackbirds and a single (?) thrush, though house sparrows, dunnocks and starlings were also involved. Of the 108 baits that were observed being eaten, only 13 were consumed by the last three species.

Results Table 22 gives the numbers of baits taken during each trial. Analysis¹ reveals significant heterogeneity in the proportions of greens and browns taken per trial in 3.1a ($\chi^2_{(5)} = 64.570$ $P < 0.001$). After changing the relative frequencies of the colours, the common browns were taken almost exclusively on each day.

If the grand totals are compared with the expected 9:1 ratios assuming random predation, it is obvious that relatively too many browns were taken from both 3.1a and 3.1b. A measure of this overall brown preference is given by:

$$\text{C.P.R., assuming constant selection} = 3.46$$

Taking this into account, we derive the expected predation shown in parentheses in Table 22. The recorded selection deviates from the expected in the direction predicted by apostasy. This effect was statistically significant:

$$\chi^2_{(1)} = 6.63, P < 0.02$$

¹The 2 baits taken in the first trial on 5.8 were pooled with the data for the succeeding trial, whilst the 5 browns taken on 12.8 were added to the results of 8.8.

Table 23 Experiment 3.4. Totals of baits taken during trials

Predators - blackbirds, starlings, housesparrows (many of each)
Background - soil

a. 90 greens: 10 browns

Date (1968)	Times (B.S.T.)	Predation	
		G	B
13.8	17.08 - 17.45	24	5 *
	21.17 - 21.32	28	5 *
14.8	10.16 - 10.38	29	8 *
	12.21 - 12.30	21	10 *
	15.15 - 15.29	12	10 *
15.8	17.01 - 17.11	14	9 *
	Grand totals	128	47
		(112.5)	(62.5)

b. 10 greens: 90 browns

Date (1968)	Times (B.S.T.)	Predation	
		G	B
16.8	13.01 - 14.15	1	31
	14.15 - 14.31	0	48 *
	14.51 - 15.10	0	53 *
	15.16 - 15.30	0	12 *
17.8	10.01 - 12.09	0	86 *
	12.15 - 13.59	0	32 *
	Grand totals	1	262
		(4.7)	(257.3)

Experiment 3.4

Method The experiment was carried out on a fallow plot (O.S. grid reference 275713) of a market-garden near Bridge End, Edinburgh. The green baits appeared more conspicuous against the soil. For obvious reasons the area was well-endowed with birds and the rate of bait-predation was correspondingly high. Many birds were observed feeding on a pile of hop-manure about 100 m from the plot.

Results Table 23 gives the results. When greens were common, the proportions taken per day were significantly heterogeneous ($\chi^2_{(5)} = 6.25$ $P < 0.05$). When browns became common they were taken almost exclusively by the birds. A comparison with expected 9:1 ratios, shows that too many browns were taken in both 3.4a and 3.4b. In other words the birds possessed frequency-independent preferences for browns:

C.P.R., assuming constant selection = 5.00

The expected predation, assuming constant selection, is shown in Table 23. In comparison, the recorded values deviate in the direction predicted by apostatic selection:

$$\chi^2_{(1)} = 9.00, P < 0.01$$

Table 24 Experiment 5.2. Totals of baits taken during daily trials

Predators - blackbirds (4)
Background - grass

a. 180 greens: 20 browns

Date (1969)	Times (G.M.T.)	Predation			
		G	B		
14.2	10.01 - 13.50	31	6	*	S
15.2	10.11 - 10.53	35	8		S
16.2	9.00 - 13.45	34	5	*	S
17.2	12.05 - 17.08	47	4	*	S
18.2	12.59 - 16.22	51	4	*	S
19.2	11.55 - 15.12	43	9	*	S
21.2	9.45 - 15.20	50	8	*	S
23.2	11.14 - 16.12	62	12		S
	Grand totals	353	56		
		(343.0)	(66.0)		

b. 20 greens:180 browns

Date (1969)	Times (G.M.T.)	Predation			
		G	B		
24.2	9.00 - 12.05	3	51		S
25.2	8.55 - 17.01	5	73		S
1.3	11.30 - 14.59	1	32	*	S
2.3	9.10 - 16.50	0	49	*	S
4.3	9.49 - 16.20	0	21	*	S
7.3	9.45 - 16.10	2	52	*	
	Grand totals	11	278		
		(17.4)	(271.6)		

Experiment 5.2

Method The grid was situated in a field (O.S. grid reference NT 294610) about one mile south of Rosewell, Midlothian. Snow covered the site for most of the experiment. Between 15th and 25th February inclusive the plot was totally covered. On the 14th February and 1st, 2nd, 3rd and 4th March snow covered about three-quarters of the area. The three days of continuous observation revealed that blackbirds were the only predators.

Results The results for daily predation are shown in Table 24. There is no evidence for heterogeneity in the numbers of greens and browns taken daily during 5.2a ($\chi^2_{(7)} = 5.47, P < 0.50$). After the compositions of the populations were changed, the birds soon began to concentrate on searching for browns.

The blackbirds had an overall preference for browns:

C.P.R., assuming constant selection = 1.73

The expected predation, assuming constant selection, is shown in Table 24 and it can be seen that the recorded values deviate in the directions predicted by apostatic selection. These deviations are statistically significant:

$$\chi^2_{(1)} = 4.32, P < 0.05$$

Table 25 Experiment 5.3. Totals of baits taken during daily trials

Predators - blackbirds (2)
Background - grass

a. 180 greens:20 browns

Date (1969)	Times (G.M.T.)	Predation		
		G	B	
17.2	11.30 - 16.01	14	8	*
18.2	10.09 - 14.59	38	7	*
21.2	10.59 - 16.25	48	10	*
23.2	9.40 - 16.59	51	8	*
27.2	12.15 - 16.52	31	2	*
2.3	10.25 - 16.30	49	5	
	Grand totals	231	40	
		(217.0)	(54.0)	

b. 20 greens:180 browns

Date (1969)	Times (G.M.T.)	Predation		
		G	B	
3.3	11.10 - 13.40	3	31	
4.3	10.15 - 17.00	2	28	*
6.3	10.10 - 16.59	0	50	*
8.3	11.30 - 17.48	1	76	*
9.3	12.50 - 16.35	0	66	*
10.3	9.59 - 16.25	1	48	*
	Grand totals	7	299	
		(4.5)	(291.5)	

Experiment 5.3

Method The grid was sited in a field (O.S. grid reference NT 261702) on a north-facing slope 50 m from the Braid Burn in Blackford Glen, Liberton, Edinburgh. Blackbirds were the only observed predators. The plot was completely covered by snow on the first five days. During the next four, patches of grass were showing, whilst for the last three days of the experiment the ground was clear.

Results Table 25 shows the daily results. The proportions taken during 5.3a were significantly heterogeneous ($\chi^2_{(6)} = 11.82$, $P < 0.05$) and during 5.3b the birds clearly tended to concentrate on predating browns.

Comparison with the expected 9:1 ratios shows that too many browns were taken from both parts of the experiment and this preference is illustrated by:

C.P.R., assuming constant selection = 2.24

The recorded predation deviates from the expected values calculated by assuming constant selection in the direction predicted by apostatic selection:

$$\chi^2_{(1)} = 8.60, P < 0.01$$

Table 26 Experiment 5.4. Totals of baits taken during daily trials

Predators - blackbirds (2)
Background - grass

a. 180 greens: 20 browns

Date (1969)	Times (G.M.T.)	Predation		
		G	B	
8.3	10.00 - 16.19	12	4	*
9.3	10.58 - 11.50	18	5	
10.3	9.07 - 15.41	29	3	*
7.4	10.05 - 17.28	31	8	*
8.4	11.01 - 14.03	23	3	*
9.4	12.15 - 17.05	33	7	*
11.4	9.56 - 14.04	46	9	
	Grand totals	192	39	
		(175.6)	(55.4)	

b. 20 greens:180 browns

Date (1969)	Times (G.M.T.)	Predation		
		G.	B	
14.4	10.02 - 16.10	3	63	
15.4	11.34 - 16.45	0	46	*
16.4	12.10 - 17.59	1	54	*
21.4	12.56 - 15.05	2	39	*
22.4	9.58 - 17.15	0	77	*
25.4	9.15 - 17.45	0	69	*
	Grand totals	6	348	
		(13.6)	(340.4)	

Experiment 5.4

Method The grid was placed in a grassy field (O.S. grid reference NT 300625) near Rosewell, Midlothian, and blackbirds were the only observed predators. As can be seen from the dates given in Table 26, the experiment was suspended for about one month three days after the start.

Results Table 26 shows the daily predation. The proportions taken during the first part of the experiment did not differ significantly ($\chi^2_{(6)} = 3.34, P > 0.70$).

Compared with 9:1 ratios, too many browns were taken from both types of population:

C.P.R., assuming constant selection = 2.84

Taking this preference into account, the recorded predation deviated from the expected in the direction predicted by apostatic selection. This effect was statistically significant:

$$\chi^2_{(1)} = 10.82, P < 0.01$$

Table 27 Experiment 6.2. Totals of baits taken during trials

Predators - blackbirds (4)
Background - grass

a. 180 greens:20 browns

Date (1969)	Times	Predation		
		G	B	
5.5	9.59 - 16.14	5	7	*
6.5	9.30 - 11.30	33	13	*
9.5	9.30 - 11.30	36	9	
10.5	14.02 - 16.30	42	7	
	16.30 - 18.00	25	8	*
11.5	9.45 - 12.10	40	16	
	12.15 - 14.30	35	9	*
	15.01 - 17.45	63	14	
19.5	9.59 - 10.20	12	5	
	10.30 - 12.16	28	8	*
	12.29 - 14.45	43	9	*
	16.28 - 17.16	13	1	
20.5	13.57 - 15.06	40	6	
	15.18 - 16.45	25	6	*
25.5	9.59 - 11.40	43	5	
	12.00 - 14.35	15	2	*
27.5	13.30 - 16.25	48	9	
29.5	9.09 - 12.12	33	6	
30.5	14.12 - 15.10	18	2	
	15.15 - 16.21	22	6	*
	Grand totals	619	148	
		(601.3)	(165.7)	

b. 20 greens:180 browns

Date (1969)	Times	Predation		
		G	B	
4.6	12.58 - 17.07	5	67	
6.6	11.39 - 12.10	0	21	
	12.20 - 14.39	0	37	*
10.6	10.15 - 11.52	0	24	
	12.15 - 14.59	1	69	*
	15.03 - 15.04	0	5	
	15.27 - 17.31	0	90	*
	Grand totals	5	313	
		(13.6)	(304.4)	

Experiment 6.2

Method The experiment was carried out on a playing field (O.S. grid reference NT 272704) at Liberton Dams, Edinburgh. Blackbirds were the only observed predators.

Results These are given in Table 27. The proportions taken per trial are not significantly heterogeneous ($\chi^2_{(19)} = 27.631$, $P < 0.05$) during 6.2a. Following the change of population composition, there may have been a tendency for the birds initially to search for greens. On the first day of presentation of 20 greens: 180 browns, 5 greens and 67 browns were taken as opposed to a total of 1 green and 256 browns for the remaining six days. These proportions are significantly different ($\chi^2_{(1)} = 13.493$, $P < 0.001$). Moreover, all 5 greens were taken during the first six visits out of a total of 15 for the day.

Overall, however, the birds took too many browns from both types of populations:

C.P.R., assuming constant selection, = 2.48

Taking this into account, the birds tended to select in an apostatic manner and this effect was significant:

$$\chi^2_{(1)} = 8.13, P < 0.01$$

Table 28 Experiment 3.2. Totals of baits taken during trials

Predators - blackbirds (4)
Background - grass

a. 10 greens: 90 browns

Date (1968)	Times (B.S.T.)	Predation		
		G	B	
1.8	11.40 - 16.15	0	45	*
	17.12 - 20.45	0	71	*
2.8	21.13(1.8) - 11.00	1	90	*
	11.28 - 15.00	0	44	*
	15.20 - 17.00	0	44	*
	17.19 - 20.15	0	88	*
3.8	20.43(2.8) - 12.45	0	90	*
	13.11 - 14.48	1	82	*
	15.18 - 20.00	0	90	*
4.8	20.32(3.8) - 12.00	0	90	*
	Grand totals	2	734	
		(4.0)	(732.0)	

b. 90 greens:10 browns

Date (1969)	Times (B.S.T.)	Predation		
		G	B	
4.8	15.40 - 16.22	1	42	
6.8	13.40 - 16.30	0	28	
9.8	11.00 - 12.40	17	13	
12.8	14.35 - 16.30	5	2	*
	16.42 - 19.07	30	7	*
13.8	9.02 - 10.01	10	10	*
	Grand totals	63	102	
		(50.5)	(114.5)	

(ii) Presentation of 1G:9B populations followed
by 1G:9B populations

Experiment 3.2

Method The grid was situated in a disused part of a playing field (O.S. grid reference NT 272704) at Liberton Dams, Edinburgh. The grass at this site was more uniform in length and colour, and more dense than in the agricultural fields used in other experiments. The only observed predators were blackbirds.

Results The numbers of baits removed during each trial are shown in Table 28. Browns were taken almost exclusively during 3.2a. On four occasions this colour was completely eradicated from the population and in only one of these cases were any greens taken - and then no more than one. The daily proportions removed from the 9G:1B populations were significantly heterogeneous ($\chi^2_{(4)} = 79.87, P < 0.001$). During the first two days the birds took almost only browns, whilst later they ate relatively more greens.

Overall, the birds took too many browns from both types of population:

C.P.R., assuming constant selection = 20.40

Taking this into account, the birds tended to predate in an apostatic manner. This effect was not, however, statistically significant:

$$\chi^2_{(1)} = 5.44, P < 0.02$$

Table 29 Experiment 3.3. Totals of baits taken during trials

Predators - blackbirds, starlings, housesparrows (many of each)
Background - soil

a. 10 greens:90 browns

Date (1968)	Times (B.S.T.)	Predation		
		G	B	
3.8	12.00 - 21.30	0	40	*
4.8	21.57(3.8) - 12.32	2	52	*
	12.48 - 15.00	0	15	*
5.8	12.00 - 14.25	0	90	*
7.8	9.01 - 14.15	0	90	*
	Grand totals	2	287	
		(5.8)	(283.2)	

b. 90 greens:10 browns

Date (1968)	Times (B.S.T.)	Predation		
		G	B	
13.8	14.05 - 14.59	15	9	*
	17.01 - 17.30	14	8	*
	20.50 - 21.15	8	7	*
14.8	9.59 - 10.11	9	10	*
	10.20 - 11.51	1	10	*
15.8	12.15 - 16.33	22	10	*
	17.01 - 18.01	24	9	*
16.8	9.09 - 9.55	10	9	*
	10.01 - 10.21	8	8	*
	10.30 - 10.45	1	10	*
	10.59 - 11.19	14	7	*
	11.30 - 11.58	8	10	*
	15.40 - 16.05	9	10	*
	16.51 - 17.08	11	10	*
	18.21 - 18.05	7	8	*
	18.10 - 18.45	6	4	*
	Grand totals	167	139	
		(159.1)	(146.9)	

Experiment 3.3

Method The grid was laid down on soil, in a separate part (O.S. grid reference NT 277713) of the market garden used in 3.4. The two plots were separated by a main road and a distance of about $\frac{1}{4}$ mile. Many birds of various species were involved in the experiment 3.3 and they were also seen feeding in a pile of hop-manure about 30 m from the grid.

Results These are given in Table 29. The birds clearly had strong preferences for browns. In 3.3a the common browns were completely eliminated on two occasions. The proportions taken per trial during 3.3b were distinctly heterogeneous ($\chi^2_{(15)} = 30.164$, $P < 0.02$).

Overall, too many browns were taken from both types of population:

C.P.R., assuming constant selection = 8.31

If this is taken into account, we find that the birds were tending to select in a frequency-dependent manner though, statistically, this effect was not significant:

$$\chi^2_{(1)} = 3.35, P > 0.10$$

Table 30 Experiment 5.1. Totals of baits taken during trials

Predators - blackbirds (4)
Background - grass

a. 20 greens:180 browns

Date (1969)	Times (G.M.T.)	Predation			
		G	B		
14.2	11.09 - 14.45	0	9	*	S
15.2	9.10 - 15.29	0	10	*	S
	16.09 - 16.29	0	11		S
16.2	11.08 - 16.00	0	35	*	S
17.2	10.00 - 15.11	1	38	*	S
18.2	11.22 - 15.49	0	68	*	S
19.2	12.50 - 16.45	0	45	*	S
21.2	12.00 - 17.10	1	69	*	S
25.2	9.21 - 17.12	1	83		S
	Grand totals	3	368		
		(13.5)	(357.5)		

b. 180 greens:20 browns

Date (1969)	Times (G.M.T.)	Predation			
		G	B		
26.2	12.45 - 16.36	28	18		S
28.3	10.05 - 13.49	42	16		S
4.3	11.25 - 17.45	59	15	*	S
5.3	12.15 - 17.32	30	12		
7.3	11.00 - 17.38	78	15	*	
8.3	10.59 - 17.10	63	9	*	
10.3	9.50 - 16.05	72	6	*	
	Grand totals	372	90		
		(348.0)	(114.0)		

Experiment 5.1

Method The experiment was carried out in a grassy field (O.S. grid reference NT 303637) at Dalhousie Chesters, near Rosewell, Midlothian. Snow completely covered the site during 5.1a and the first two days of 5.1b. On the third day only a few patches of snow were left and by the next day it had completely melted. Blackbirds were apparently the only predators.

Results The predation during trials is given in Table 30. As with other experiments, the proportions of browns predated were very high when these baits were common. When greens were common, in 5.1b, the daily proportions taken were heterogeneous ($\chi^2_{(6)} = 26.21$, $P < 0.001$). In addition, there was a significant increase in the percentage of greens taken over the duration of 5.1b (Spearman's rank correlation coefficient = 0.8129, $P < 0.05$).

The grand totals show that relatively too many browns were removed from both types of population:

C.P.R., assuming constant selection = 2.95

When this overall brown preference is taken into consideration it is found that the recorded predation deviates from the expected in the direction predicted by apostatic selection:

$$\chi^2_{(1)} = 15.18, P < 0.001$$

Table 31 Experiment 5.5. Totals of baits taken during daily trials

Predators - blackbirds (5)
Background - grass

a. 20 greens:180 browns

Date (1969)	Times (G.M.T.)	Predation		
		G	B	
7.4	9.10 - 16.49	0	35	*
8.4	12.00 - 17.15	0	48	*
9.4	13.11 - 17.50	0	46	*
11.4	15.02 - 17.08	0	22	*
14.4	9.10 - 16.40	2	59	*
15.4	12.20 - 16.10	0	89	*
16.4	13.08 - 17.10	1	51	
	Grand totals	3	350	
		(14.2)	(338.8)	

b. 180 greens:20 browns

Date (1969)	Times (G.M.T.)	Predation		
		G	B	
17.4	13.01 - 17.05	20	39	
18.4	11.09 - 16.05	58	27	
19.4	9.30 - 17.10	79	13	
21.4	13.40 - 16.07	21	5	*
22.4	11.10 - 17.50	83	3	*
23.4	12.55 - 17.15	40	5	*
24.4	10.00 - 18.10	60	8	
	Grand totals	380	81	
		(356.1)	(104.9)	

Experiment 5.5

Method The grid was situated on a lawn (O.S. grid reference NT 268706) adjacent to the Department of Engineering, Kings Buildings, University of Edinburgh. Blackbirds were the only apparent predators.

Results The daily numbers of baits taken are given in Table 31. After an almost monotonous diet of browns in 5.5a, the birds also took relatively too many of this colour when rare in 5.5b. The proportions taken daily were significantly heterogeneous ($\chi^2_{(6)} = 100.454$, $P < 0.001$).

A measure of the brown preferences is given by:

C.P.R., assuming constant selection = 2.65

Taking this into account, the birds tended to predate in an apostatic manner:

$$\chi^2_{(1)} = 16.24, P < 0.001$$

Table 32 Experiment 6.1. Totals of baits taken during trials

Predators - blackbirds (4)
Background - grass

a. 20 greens: 180 browns

Date (1969)	Times	Predation		
		G	B	
7.5	14.15 - 15.20	0	18	
	15.30 - 17.29	1	16	*
8.5	14.20 - 15.10	0	23	
	15.15 - 18.11	1	55	*
12.5	11.15 - 11.29	0	6	
	11.30 - 18.41	1	110	*
13.5	9.10 - 9.12	0	9	
	9.16 - 12.00	0	85	*
18.5	10.37 - 13.49	0	56	*
	14.09 - 14.10	0	2	
	14.15 - 18.05	1	89	*
22.5	9.59 - 11.39	0	35	
	11.42 - 12.00	0	50	*
25.5	14.10 - 17.00	0	52	
	Grand totals	4	606	
		(16.5)	(593.6)	

b. 180 greens: 20 browns

Date (1969)	Times	Predation		
		G	B	
26.5	10.15 - 17.15	84	54	
28.5	14.00 - 15.14	7	12	
	15.16 - 17.18	37	11	*
2.6	14.15 - 14.45	7	2	
	14.52 - 17.20	70	10	*
3.6	10.30 - 12.01	29	12	
	12.15 - 14.10	33	5	*
5.6	14.21 - 18.59	46	9	*
9.6	15.19 - 18.49	41	7	*
13.6	10.09 - 17.15	59	9	*
	Grand totals	411	131	
		(375.4)	(166.6)	

Experiment 6.1

Method The experiment took place in a grassy field (O.S. grid reference NT 302618) near Capielaw Farm, Rosewell, Midlothian. Again, blackbirds were apparently the only predators.

Results The numbers taken during each trial are shown in Table 32. When browns were common predation was almost exclusive to this colour. During 6.1b, when greens were common, the proportions taken per trial were significantly heterogeneous ($\chi^2_{(9)} = 50.50$, $P < 0.001$). Note the high percentage of browns taken on the first day (26th May).

A measure of the brown preferences is given by:

C.P.R., assuming constant selection = 3.99

Taking this into account, the recorded predation deviated from the expected in the direction predicted by apostatic selection.

This effect was statistically significant:

$$\chi^2_{(1)} = 20.72, P < 0.001$$

CHAPTER VII THE RESPONSES OF INDIVIDUAL TURDIDAE:

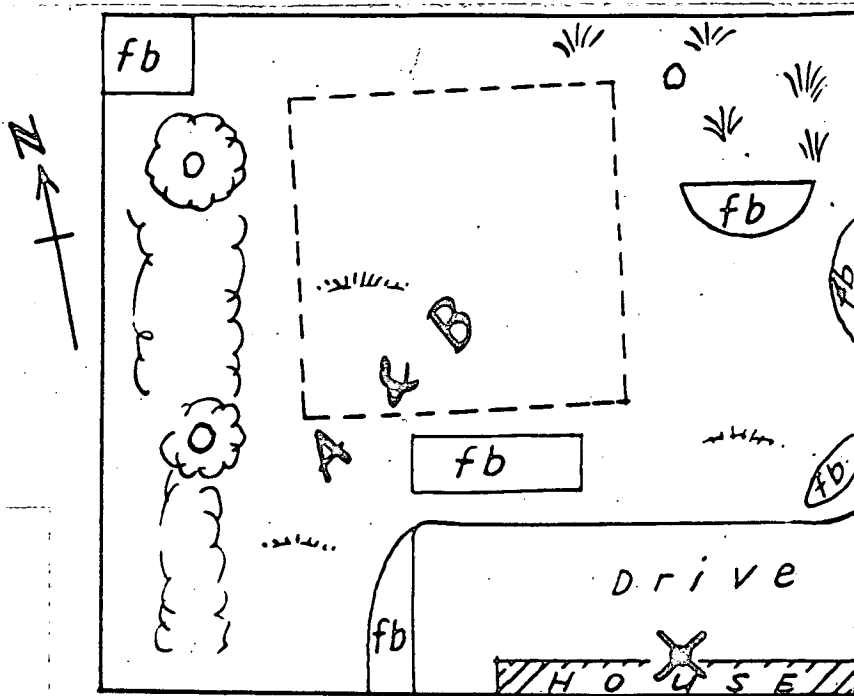
PART 1

Figure 10

and VII

Sites of plots in experiments 2.1 (Chapters VI) and 2.2, 2.3 (Chapter VIII), showing boundaries of blackbird territories

a. Experiment 2.1 (January - February 1967)



KEY

--- outline of plot.

— bush

o — tree

fb — flower bed

— lawn

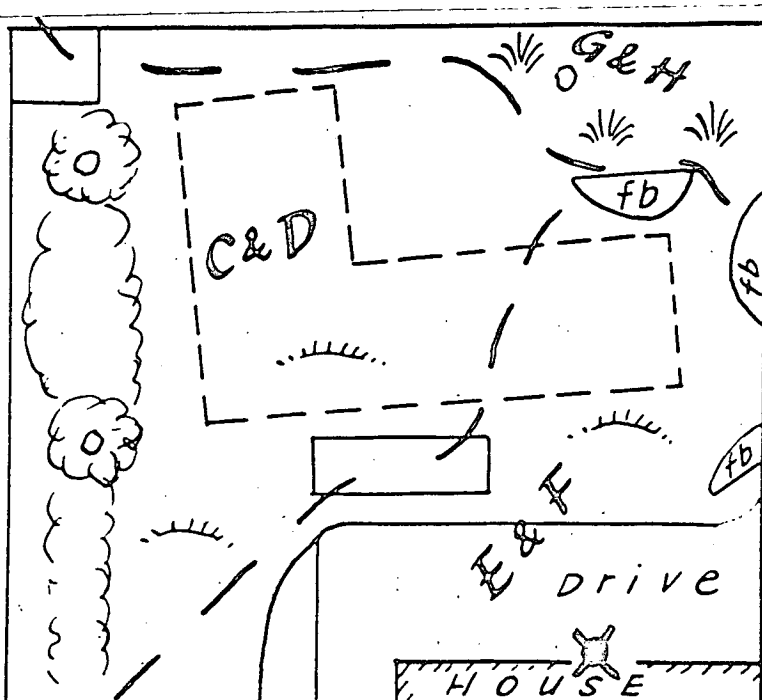
— long grass

— territorial boundary

x — observation point

Scale
0 5 10 Metres

b. Experiments 2.2 (March - April 1967) and 2.3 (January - February 1968)



CHAPTER VII THE RESPONSES OF INDIVIDUAL TURDIDAE: PART 1

1. INTRODUCTION

The results of the first 9:1 experiment (Chapter VI, this thesis; also Allen 1967, Allen and Clarke 1968) revealed heterogeneity between the proportions taken by blackbirds per visit. This effect may have been a result of differences between the behaviour of individual birds, but this possibility was untestable because the birds could not be reliably identified. In the experiments described in this and the following Chapter all the Turdus individuals were colour-ringed.

Three sets of experiments (2.1, 2.2, 2.3) were completed at the same site. This Chapter first describes the general details of procedure and the results of experiment 2.1 are then presented and discussed.

2. EXPERIMENTAL AREA AND BASIC MATERIALS AND METHODS

(a) Experimental procedures

The experiments were carried out on a lawn of my Reading home (O.S. grid reference SU 716765). Figure 10 shows the general topography of the area. The lawn consists of about sixty per cent grass and forty per cent daisy (Bellis perennis L.) and plantain (Plantago media L.). A skewer-marked grid of 100 metre-squares was placed on the lawn in approximately the same position in each experiment. In experiment 2.1 it was square; in the subsequent studies it was 'L'-shaped. Observations were made from behind cover in a porch of the house. The populations were maintained in the normal manner (see Chapter III) and data were recorded exactly as outlined on pages 60-61.

Results were obtained for each individual blackbird and songthrush and for predation by groups of dunnocks, robins and house sparrows (see below). The populations were continuously observed and they were usually presented from dawn to dusk. Hence a complete history of behaviour was built up for each bird.

Particular attention was paid to 'imprint-pecking'. This term describes the habit of some blackbirds and thrushes to pick up a bait and then drop it. The result of this action is a bait imprinted with the bird's beak - hence 'imprint pecking'. The term is simply one of convenience: it describes the act, not its cause.

(b) Birds

The blackbirds frequently showed territorial behaviour and from the positions of their conflicts it was possible to estimate the approximate boundaries of their territories. These are shown in Figures 10a and 10b. An important point to notice is that most or all of the plot in each experiment was under the rule of a single pair of blackbirds. All intruding birds were liable to be put to chase. This particularly applied to blackbirds and, to a lesser extent, to songthrushes. The interlopers had little time to choose their prey when they were under attack.

Colour-ringing of the Turdidae was carried out at various times, but most of the birds were ringed before the starts of the experiments (see Allen 1967, Table XIV). The majority of the birds were caught in a hand-made 'lobster-pot' trap baited with 'Swoop' and/or bread. Dunnocks, robins and house sparrows were also colour-ringed but though some of these birds were observed

feeding on the baits, accurate recognition of individuals was difficult. This was mainly because of the relative sizes of their rings and the swiftness of their feeding (particularly with regard to robins).

(c) Environmental variables

(i) Temperature. The temperature at noon was recorded for every experimental day. During experiment 2.1 (January - February 1967) the weather was exceptionally mild for the time of year and a mean of 9.6°C was recorded. For 2.2 (March - April 1967) the mean mid-day temperature was 10.3°C and for 2.3 (January - February 1968), 6.7°C .

(ii) Available natural food. Despite the relatively high average air-temperatures recorded during the two winter experiments, the ground often remained frozen. Worms, the main diet of lawn-feeding Turdidae, were therefore inaccessible. It would seem that the birds relied on baits as a main source of food, for rarely were they observed feeding otherwise.

In contrast, the birds of 2.2 (particularly the 'resident' pair) frequently entered the plot and ignored the baits, preferentially hunting for worms. No accurate assessment was made of the numbers of worms taken.

(iii) Rain. The work was never curtailed by heavy rain; observations were always continued, although the birds tended to visit the plot less frequently. Snow was never observed to settle, though on some early mornings the ground was covered by frost.

(iv) Grass. In the winter experiments the grass was not growing but was 'long'. On average, the blades were probably about 3 cm long, and of course not all were vertical. Four days before the start of 2.2 the lawn was mown and by the end of the experiment the grass had grown to the length it had been in 2.1.

3. EXPERIMENT 2.1¹ 1G:9B POPULATIONS FOLLOWED BY 9G:1B AND OTHER 'GREEN-DOMINATED' POPULATIONS

This study has been described briefly in Chapter VI in connexion with the overall predation. Here we consider the birds individually. Two blackbirds and a songthrush were presented with 1G:9B populations succeeded by 9G:1B and other types of populations containing successively fewer frequencies of browns.

(a) Chronology

The dates of presentation of the populations were as follows:

a. From 16 to 23 January (inclusive)	: 20 greens + 180 browns
b. From 24 January to 31 January (inclusive)	: 180 greens + 20 browns
c. On 1 and 2 February	: 192 greens + 8 browns
d. On 3 February	: 196 greens + 4 browns
e. On 4 February	: 199 greens + 1 brown

The reasoning behind the presentation of the successively lower frequencies of brown will be clarified shortly.

(b) Materials and methods

Figure 10a shows the position of the grid situated within the territory of a male colour-ringed blackbird (A) and his mate (B).

¹This experiment formed part of a B.Sc. Honours project (Allen 1967) and is included here for completeness.

Table 33

Experiment 2.1. Grand totals of baits eaten and imprint-pecked (shown in parentheses) by blackbirds A (♂), B (♀) and songthrush T (♂).

Population	Inclusive dates of presentation (1967)	BLACKBIRDS				THRUSH	
		A		B		T	
		G	B	G	B	G	B
a. 20G + 180B	16.1 - 23.1	0 -	125 -	1 (2)	122 (0)	0 -	65 -
b. 180G + 20B	24.1 - 31.1	1 (11)	130 (0)	91 (12)	21 (0)	0 -	176 -
c. 192G + 8B	1.2 - 2.2	0 (2)	30 (0)	32 -	0 -	0 -	33 -
d. 196G + 4B	3.2	15 (29)	2 (0)	12 -	0 -	0 -	21 -
e. 199G + 1B	4.2	20 (1)	0 (0)	20 -	0 -	11 (3)	0 (0)

These birds along with a male thrush (T), were the main predators.

(c) Results

(i) Summary of data

Table 33 condenses the results for the individual Turdidae¹. The complete daily results are given in Table 36 in Appendix B, page 161 (from Allen 1967, Table IV). The plain figures represent the numbers of baits consumed by each bird over the periods of presentation. Figures in parentheses represent the grand totals of imprint-pecked baits over the corresponding periods.

The birds clearly differed in their individual responses. Although they all took an excess of browns from the 1G:9B populations, only one bird, B, took appreciable proportions of greens from 9G:1B populations. Blackbird A and the Thrush T consumed browns almost exclusively. It was for this reason that the relative proportions of browns were subsequently lowered. In other words the birds' preferences for browns had led to the question: how low must be the frequency of browns before A and T are forced to eat greens? Or more simply, how 'strong' are their brown preferences?

As can be deduced from Table 33, A switched to feeding on greens when there were only 4 browns within the plot whilst T did not relax his brown preference until only 1 brown was available. It will also be noted that the relative incidence of green imprint-pecking in these birds was highest on the days when the behavioural switches occurred. Of B's 12 green imprint-pecks, 4 occurred on the day when she first started to take the common greens (24.1.67) and 5 took place on the second (see Table 36, page 161). We shall now examine the individual responses in greater detail.

¹Robins and dunlocks took greens alone from the four types of green-dominated population (79 greens and 9 greens, respectively). Neither species removed any baits from the 1G:9B populations.

(ii) Apostatic selection

We noted in Chapter VI (page 108) that overall, the birds did not exhibit significant frequency-dependent selection. Let us now examine the results for parts a. and b. with regard to the data for individuals.

On the basis of the 9:1 ratios it is clear that all the birds took too many browns from both types of populations. A and T were obviously not preying apostatically, for in both parts of the experiment they ate browns almost without exception. B, on the other hand, took appreciable numbers of greens during the presentation of 180G + 20B. Her results can therefore be tested for frequency-dependence, using the method described on page 104. Once again, however, we are faced with the problem of heterogeneity within the proportions taken per day. This point is made by the relevant data shown in Table 36 (page 161), though these are not amenable to analysis by the chi-squared test.

Nevertheless, if we assume selection to be constant in parts a. and b. of the experiment, then we can derive the expected values for the grand totals as shown in Table 34. These differ from the expected in the direction predicted by apostatic selection and this effect was statistically significant ($\chi^2_{(1)} = 5.45$ $P < 0.02$). The female blackbird appears to have been predating in an apostatic manner.

Table 34

Observed and expected (assuming constant selection) grand totals of baits taken by blackbird B during parts a. and b. of experiment 2.1. The expected values are shown in parentheses.

	G	B
a.	1 (4.24)	122 (117.76)
b.	91 (83.24)	21 (28.76)

Diminution of brown-preferences in blackbirds A, B and songthrush T. Sequences of baits eaten and imprint-pecked per visit during the transitional periods. Visits are numbered from the start of presentation of 20 greens + 180 browns. Imprint-pecked baits are shown in ordinary parentheses. Symbols within square brackets pertain to the same bait. Thus on his 97th visit after 'ratio-reversal', T imprint-pecked a green before picking it up and eating it.

Table 35a Blackbird B

Visit	24.1.67 Order of selection			Visit	25.1.67 Order of selection		
	1	2	3		1	2	3
1	b			14	g		
2	b			15	(g)	g	
3	b			16	g		
4	(g)	b		17	g		
5	b			18	g	g	
6	b			19	g		
7	(g)	(g)		20	(g)		
8	g			21	b		
9	g	g	g	22	g		
10	b			23	g	(g)	
11	g			24	g	g	g
12	b			25	g	g	
13	(g)	g		26	g	g	g

Table 35b Blackbird A (3.2.67)

Visit	Order of Selection																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
97	(g)	b															
98	b																
99	(g)	(g)	(g)	(g)													
100	[(g)	(g)	(g)	(g)	(g)	(g)	(g)	(g)	(g)	g]	[(g)	(g)	(g)	(g)	(g)	(g)	g]
101	[(g)	(g)	g]	(g)													
102	(g)	(g)	g	g													
103	g	g															
104	(g)	(g)	(g)	g	g												
105	(g)	g	g														
106	g	g															

Table 35c Thrush T (4.2.67)

Visit	Order of selection					
	1	2	3	4	5	6
93	nothing taken					
94	"			"		
95	"			"		
96	"			"		
97	[(g)	g]				
98	[(g)	g]				
99	[(g)	g]	g	g	g	g
100	g	g	g	g		

(iii) Relaxation of brown preferences

As already mentioned the birds did not immediately stop searching for browns when these baits became rare. Blackbird B was the only predator to switch to searching for greens as well as browns on the first day. The evolution of this change is shown in Table 35a which gives the sequences of baits taken per visit during 24 and 25 January. It will be noted that the first three greens selected (on visits 4 and 7) were not eaten, but merely picked up and dropped (imprint-pecked).

Blackbird A and the songthrush continued to search for browns. The blackbird in fact imprint-pecked a total of 11 baits during the presentation of 180 greens + 20 browns; three of these occasions were on the first day after ratio reversal (24.1.67) and five occurred six days later (29.1.67). On his twelfth visit (25.1.67) he actually ate one green bait without hesitation (see Table 36). The thrush meanwhile appeared to disregard the greens entirely.

As the relative proportions of browns were lowered, A was the first of the two male birds to lose his obvious brown preference. This took place on 3.2.67, when the population contained 196 greens + 4 browns. Table 35b gives the results for A on this day and shows the sequences in which the baits were eaten and imprint-pecked on each of the ten visits. As can be seen, the bird ate his first greens (apart from the single instance mentioned above) on the fourth visit. From then on, greens were taken freely. This transition was not clear-cut, for the predation of greens was preceded by a relatively high incidence of green-imprint-pecking. Such behaviour involved either different baits (as on visit 99), or the same one (e.g. visit 100). On the succeeding final day of

the experiment, A imprint-pecked a single green and ate 20 more without hesitation.

The male thrush totally neglected the greens until the last day, when the population consisted of 199 greens + 1 brown. Table 35c illustrates the behaviour of the bird on this day. On his first four visits he searched all over the plot (see Fig. 14(b), Allen 1967) without finding the lone brown bait. Nevertheless he discovered about three minute pieces of brown dough that had probably fallen to the ground during 'replacing'. Once again the onset of green predation was accompanied by imprint-pecking. The first three greens eaten were all imprint-pecked once before consumption.

(d) Discussion

We remarked in Chapter VI (p. 108) that the three birds as a group did not select in a frequency-dependent manner and, assuming homogeneous behaviour, it could be inferred that the same conclusion applies to the birds as individuals. This is refuted by a closer examination of the data, for one blackbird (B) tended to take the commoner colours. On the other hand blackbird A and songthrush T were strongly biased to take brown baits alone and irrespective of their frequency. Even these two birds were not alike in their behaviour; A started taking greens when four browns were present while T did not start until the population contained only one brown and then not until after he had unsuccessfully searched the plot on four separate occasions. The behaviour of the birds therefore ranged from B to A to T, in order of increasing strength of their brown preferences. It may be relevant that B, the only bird to start eating appreciable numbers of browns on the first day in 2.1b, was the only bird that had had experience of greens in 2.1a.

The three birds therefore differed in their responses. They also had other idiosyncrasies; for instance with regard to imprint-pecking, particularly when they were starting to feed on greens in quantity. This can be seen from a comparison between Tables 35a, b, c. Other differences of behaviour were less measurable. For example, blackbird A appeared to exhibit a form of imprint-pecking in addition to the normal type. On these occasions the bird would crouch, bend its neck and simply nip the side of the bait as it lay on the ground. This behaviour was recorded only on 29.1.67, when it occurred five times (see also Allen 1967). Blackbird B never behaved in such a manner and T but once, in experiment 2.2 (see Table 42, p.195).

It will be noted that in two birds the incidence of green imprint-pecking increased markedly just before their switch to green-feeding. We shall further consider this point later (p.183 ff).

All the other 9:1 experiments described in Chapter VI gave evidence that predation by groups of birds tends to be apostatic. I suggest that the present results were due to the small sample of predators involved, which by chance happened to contain two individuals with very strong preferences for browns. The effect of these birds masked the effect of the tendency of B to choose the commoner sorts. The argument that the present findings are the exception rather than the rule is supported by the fact that the other thirteen experiments all gave results in the direction predicted by apostatic selection.

Further discussion of the brown preferences and the variability of behaviour will be delayed until the end of Chapter VIII, after the results of experiments 2.2 and 2.3 have been presented.

(e) Conclusion

This experiment raised some interesting questions, for example:

- (i) Why do blackbirds and songthrushes prefer browns, if such behaviour is widespread?
- (ii) To what extent were the strong brown preferences in 2.1b, c and d due to searching images acquired during exposure to the 9G:1B populations of 2.1a?
- (iii) Is the behaviour within a group of Turdus individuals always as heterogeneous as in the group in experiment 2.1? If so, what is the cause of the variability?

A control experiment starting with the presentation of 9G:1B populations was required to help answer these questions.

APPENDIX B: TABLE 36

Full results for experiment 2.1., Chapter VII

Date (1967)	BLACKBIRDS						THRUSH		
	A			B			T		
	G	B	v	G	B	v	G	B	v
a. 20 greens + 180 browns									
17.1	-	-	-	-	-	-	-	-	-
18.1	0	24	11	1	34	15	-	-	-
19.1	0	19	10	(2) + 0	30	18	-	-	-
20.1	0	16	10	0	16	10	0	6	3
21.1	0	21	12	0	15	13	0	18	9
22.1	0	24	14	0	15	11	0	19	7
23.1	0	21	10	0	12	11	0	22	8
Grand totals	0	125	67	(2) + 1	122	78	0	65	27
b. 180 greens + 20 browns									
24.1	(3) + 0	18	9	(4) + 6	8	13	0	13	8
25.1	1	16	9	(5) + 17	1	14	0	23	9
26.1	0	16	11	(1) + 17	1	11	0	20	9
27.1	0	9	6	5	1	4	0	23	7
28.1	(1) + 0	15	10	(1) + 9	1	4	0	29	10
29.1	(6) + 0	14	8	12	0	4	0	22	6
30.1	0	18	10	16	3	11	0	29	8
31.1	(1) + 0	24	12	(1) + 9	6	10	0	17	5
Grand totals	(11) + 1	130	75	(12) + 91	21	71	0	176	62
c. 192 greens + 8 browns									
1.2	0	17	10	15	0	9	0	16	7
2.2	(2) + 0	13	10	17	0	8	0	17	10
Grand totals	(2) + 0	30	20	32	0	17	0	33	17
d. 196 greens + 4 browns									
3.2	(29) + 15	2	10	12	0	7	0	21	13
e. 199 greens + 1 brown									
4.2	(1) + 20	0	11	20	0	9	(3) 0	10	
							+ 11		

CHAPTER VIII THE RESPONSES OF INDIVIDUAL TURDIDAE:

PART 2

CHAPTER VIII THE RESPONSES OF INDIVIDUAL TURDIDAE: PART 2

1. INTRODUCTION

Experiments 2.2 and 2.3a,b were essentially similar to the previous study except that they started with the presentation of 9G:1B populations. These two sets of experiments are considered simultaneously. In experiments 2.3c,d,e an extra morph was added to the system and this section of the work is presented separately.

The experimental site and the general materials and methods were described in the previous Chapter.

2. EXPERIMENT 2.2¹: 9G:1B POPULATIONS. EXPERIMENT 2.3
(PARTS a,b): 9G:1B POPULATIONS FOLLOWED BY 1G:9B
POPULATIONS

These studies were of comparable design and involved the same Turdidae, with the exception of one individual.

(a) Chronology

The dates of presentation of the populations were as follows.

Expt. 2.2. From 20th March to 3rd April 1967 (inclusive):
180 greens + 20 browns

Expt. 2.3a. From 16th January to 31st January 1968 (inclusive):
180 greens + 20 browns

b. 1st February and 2nd February 1968: 20 greens + 180 browns
(for c,d,e see page 175).

(b) Materials and methods

Experiment 2.2. By March 1967, the local blackbird population had changed drastically (Figure 10b, p. 147), though songthrush T was still in the vicinity. Blackbirds A and B had disappeared from the

¹This experiment formed part of a B.Sc. Honours project (Allon 1967).

Table 37

Experiments 2.2 and 2.3a,b. Grand totals of baits eaten and imprint-pecked (shown in parentheses) by blackbirds C (♂), D (♀), E (♂), G (♂) and songthrush T (♂). Expected predation, on the basis of 9:1 ratios is also shown for each bird.

	Popn.	Incl. dates of present- ation.	B L A C K B I R D S										THRUSH T	
			C		D		E		G					
			G	B	G	B	G	B	G	B			G	B
2.2	180G + 20B	20.3.67 - 3.4.67	97 (184)	113 (151)	140 (30)	57 (5)	158 (32)	6 (1)	24 (1)	5 (2)			7 (6)	117 (1)
		9:1	189.0	21.0	177.3	19.7	147.6	16.4	26.1	2.9			111.6	12.4
2.3a.	180G + 20B	16.1.68 -31.1.68	101 (58)	21 (19)	178 (10)	59 (6)	72 (3)	15 (1)	153 (7)	16 (4)			-	-
		9:1	109.8	12.2	213.3	23.7	78.4	8.7	152.1	16.9			-	-
b.	20G + 180B	1.2.68 -2.2.68	0 (3)	21 (22)	1 -	27 -	1 -	16 -	4 -	43 -			-	-
		1:9	2.1	18.9	2.8	25.2	1.7	15.3	4.7	42.3			-	-

area and newcomers C (male) and D (female) patrolled most of the grid. At the start of the experiment the grid was the same size and shape as in experiment 2.1. On the third day a male blackbird E periodically attempted to feed on baits in the eastern perimeter but was invariably chased away by one or both of the 'resident' pair. The shape of the plot was therefore altered so that this bird would have greater opportunity of feeding on the baits. The songthrush was also subject to attack from C or D, as was another male blackbird (G) which regularly entered the grid from a territory situated to the north (Fig. 10b). Dunnocks fed on the populations towards the end of the experiment.

Experiment 2.3a,b. Ten months later the blackbirds still appeared to be occupying the same territories, but T had since left the area. Dunnocks, robins and house sparrows also fed on the baits.

(c) Results

(i) Summary of data

Table 37 gives the grand totals of baits eaten and imprint-poached during experiments 2.2 and 2.3a,b. The expected grand totals of baits eaten, assuming 9:1 ratios, are also shown. The data refer to the five colour-ringed Turdidae only: the complete daily results for these and other birds (robins, dunnocks and house sparrows) are shown in Table 42, page 195 (from Allen 1967, Table VIII) and Table 43, page 196.

In the following pages attention will be concentrated mainly on experiments 2.2 and 2.3a. The results for 2.3b imply that all the Turdidae predated relatively too many browns, but the total numbers removed are small and do not allow meaningful conclusions.

(ii) Predation

We first examine the proportions of greens and browns that were actually eaten. Our interest centres around two main questions. First, do different birds tend to take similar proportions, or otherwise? Second, does the same bird tend to take similar proportions from two near-identical experiments separated by an interval of ten months? But before these questions are answered it is necessary to establish whether any sources of heterogeneity are being concealed by the overall results shown in Table 37.

Experiment 2.2

Heterogeneity between days. Statistical analysis for heterogeneity is hampered by the fact that each bird took low numbers of baits per day. Nevertheless an examination of the data shown in Table 42 does appear to reveal such heterogeneity in at least three birds. For example, all 6 of the browns that were eaten by E were taken during the last two days of the experiment. C appeared to eat an appreciable majority of browns on some days and of greens on others. Indeed the data suggest that this bird took progressively higher percentages of greens as the experiment proceeded (see also Allen 1967, Fig. 15a). This bird's main change of behaviour appeared to occur on the tenth day (29.3.67). Previous to this time, the percentages of browns eaten had never reached 50%, whilst afterwards the percentage predation always exceeded 67%. If we pool the daily results within each of these two periods we obtain the data shown in Table 38. The two proportions of eaten baits are clearly different.

Table 38

Male blackbird C. Numbers of baits eaten and imprint-pecked (in parentheses) during the first 9 days and last 5 days of experiment 2.2.

	G	B
20.3.67 - 28.3.67	27 (90)	100 (129)
29.3.67 - 3.4.67	70 (94)	13 (22)

D, like her mate, also commenced by concentrating on browns. Though appearing to adapt quickly to a green-biased diet (on the second day), she occasionally seemed to relapse into taking relatively higher proportions of browns (e.g. on 24.3.67 and 30.3.67).

Overall responses. It is clear from Table 37 that the Turdidae differed in their individual overall responses. Three of the birds (C, D, T) ate relatively far more browns than expected on the basis of random predation and the different proportions of baits eaten by these birds are certainly not homogeneous. The overall preferences for brown range, in order of decreasing magnitude, from T's obvious preoccupation with this colour (though not as pronounced as in 2.1a), to the more catholic responses of C and D. The male blackbird G also ate a relative excess of browns, but this effect was probably¹ not significant ($\chi^2_{(1)} = 1.69$). E, on the other hand, consumed relatively more greens than expected ($\chi^2_{(1)} = 7.33$, $P < 0.001$)¹. Moreover, as mentioned above, all 6 of these baits were taken on the last two

¹Bearing in mind the probable existence of heterogeneity within the overall results.

days of the experiment; during the preceding ten days, the bird ate 144 greens and no browns. This blackbird was unique in the history of all my '9:1 spaced-out' experiments: it was the only individual that appeared to acquire a preference for greens.

Experiment 2.3a: comparison with 2.2

Heterogeneity between days. In contrast with their behaviour in the earlier experiment, C and D did not exhibit strong brown preferences at the start of 2.3a. On this occasion C showed no tendency to eat successively higher percentages of greens with time. Neither did any other bird, whether for greens or browns. The daily results nevertheless appear to be heterogeneous, at least for C and D (e.g. note the relatively high proportions of browns taken by C on 27.1.68 and by D on 24.1.68, 25.1.68 and 27.1.68 - Table 43).

Overall responses. Direct comparison of the proportions of baits taken by each bird in 2.3a with the proportions taken in 2.2 reveals that the overall behaviour of two of the birds had apparently changed significantly (C, $\chi^2_{(1)} = 42.93$, $P < 0.001$; E, $\chi^2_{(1)} = 12.21$, $P < 0.001$; D, $\chi^2_{(1)} = 0.896$, N.S.; G, $\chi^2_{(1)} = 1.58$, N.S.). As can be deduced from Table 37, selection by C and E in 2.3a was now closer to random sampling. We have previously noted that these two predators underwent marked changes of behaviour during 2.2. Thus C's brown preference decreased during the course of the experiment, whilst E started to feed on browns only at the end of the study. We should therefore compare the predation by C in 2.3a with that during each of his brown-orientated and green-orientated phases in 2.2. The

Table 39

Comparison between overall proportions eaten and imprint-pocked (in brackets) by blackbirds C,D,E,G and songthrush T in experiments 2.2 and 2.3a.

Expt.	BLACKBIRDS								THRUSH	
	C		D		E		G		T	
	G	B	G	B	G	B	G	B	G	B
2.2	97 (184)	113 (151)	140 (30)	57 (5)	158 (32)	6 (1)	24 (1)	5 (2)	7 (6)	117 (1)
$\chi^2_{(1)}$ P	3.944 <0.05		3.256 not sign.		0.0312 not sign.		- -		47.53 <0.001	
2.3a	101 (58)	21 (19)	178 (10)	59 (6)	72 (3)	15 (1)	153 (7)	16 (4)	-	-
$\chi^2_{(1)}$ P	1.635 not sign.		1.250 not sign.		- -		7.56 <0.01		- -	

first pair of proportions differ significantly ($\chi^2_{(1)} = 94.29$, $P < 0.001$) whilst the second pair do not ($\chi^2_{(1)} = 0.085$).

Similarly, the proportions taken over E's first ten days in 2.2 differ significantly from the proportions eaten during the whole of 2.3a ($\chi^2_{(1)} = 26.56$, $P < 0.001$). The proportions consumed over the last two days do not so differ ($\chi^2_{(1)} = 1.68$).

Despite the heterogeneity between days, the findings imply that two birds, D and G, tended to select approximately the same proportions of baits during experiment 2.3a as they did in 2.2. Although a comparison of the overall results of C and E did not reveal such an effect, their responses during 2.3a appeared to duplicate their behaviour in the later stages of 2.2. The two responses of any given bird in the experiments were therefore somewhat similar. Yet the experiments were separated by a period of ten months.

(iii) Imprint-pecking

The grasping and dropping of a bait has been termed 'imprint-pecking' (p. 149). It is clear from the data given in Table 37 (page 164) that C was more prone to imprint-peck than any of his companions. This is a reflection of the bird's hesitant attitude towards the baits; each bait was usually imprint-pecked at least once before it was finally consumed or neglected.

Table 39 compares the overall proportions of imprint-pecks with the overall proportions of baits actually eaten for those cases where the data are sufficient. In four out of seven instances the proportions do not differ significantly, suggesting that on these occasions the responses of the birds when imprint-pecking were similar to when they were actually consuming the baits.

Three birds (blackbirds C, E and songthrush T) imprint-pecked in different proportions from when baits were eaten. In the case of T relatively too many greens were imprint-pecked. This bird had a strong preference for browns but the data given in Table 42, page 195, suggest that he was starting to search for greens towards the end of experiment 2.2. The data are few, but imply that the green imprint-pecking tended to occur prior and during this period of transition. The relevant data for blackbird G in 2.3a are also deficient and in this instance relatively too many browns were imprint-pecked, all within the first half of the experiment. During 2.2, except towards the end, this bird had preferred greens and it is possible that the relatively high incidence of imprint-pecking in 2.3a was related to this fact.

The results given in Tables 42 and 43 (pages 195 and 196) suggest that some birds exhibited considerable variation between days in the proportions of imprint-pecks. A closer examination of the results for blackbird D in experiment 2.2 (Table 42) reveals that of the 30 green imprint-pecks, a total of 13 occurred on the second and third days, corresponding with the noticeable increase in the proportions of greens eaten by the bird.

The heterogeneity of the data for some of the birds renders the use of the chi-squared test in Table 39 statistically 'illegal'. For C however the problem can be partly overcome by partitioning the data into the first ten and last six days. If this is done (Table 38, p. 167) we find that during the first period the proportion of imprint-pecks differs significantly from the proportion eaten ($\chi^2_{(1)} = 14.03$, $P < 0.001$), while for the second period the proportions do not differ significantly ($\chi^2_{(1)} = 0.529$). During the first period,

as noted previously, the bird appeared to be gradually losing its preference for browns.

The behaviour of C, G, T and D therefore somewhat resembles that of A and T in experiment 2.1 described in the last Chapter. That is, the start of large-scale predation on an unfamiliar colour tends to be preceded and accompanied by an increase in the incidence of imprint-pecks on this colour.

(iv) Short-term preferences

The data are not readily amenable for testing whether the predators were hunting by searching image, for the birds took few baits per visit in both experiments, as may be deduced from the daily results given in Tables 42 and 43. Often only one bait was taken. Hence the data for each visit cannot be analysed for the existence of runs (if a given bird is hunting by searching image we would expect a tendency for greens to follow greens and browns to follow browns).

As already noted, however, some of the birds appeared to take relatively large proportions of browns on certain days. Conversely, relatively high frequencies of greens seemed to be taken on other days. A superficial examination of the data revealed that the baits appeared to be taken in runs during these days. For example if a single brown was eaten by a bird on one visit, the chances were that a brown would be taken first during the next visit.

The numbers of baits taken daily are not large enough for meaningful analysis, but we can utilise the whole of the data for each experiment. For each bird we can count the number of times a bait is followed by one of the same colour and the number of occasions different colours are taken in succession. Knowing the grand totals of baits taken it is a simple matter to estimate the

Table 40

Experiments 2.2a and 2.3b. Observed and expected (in brackets) numbers of sequences of like baits (green following green and brown following brown) and unlike baits (green following brown and brown following green).

BIRD	EXPT.	SEQUENCES		$\chi^2_{(1)}$	P
		LIKE	UNLIKE		
C	2.2	79 (77.35)	40 (39.64)	0.0086	not signif.
		56 (56.82)	21 (20.18)	0.0451	not signif.
	2.3	85 (79.50)	28 (33.50)	1.2634	not signif.
D	2.2	117 (107.06)	65 (74.94)	2.241	not signif.
	2.3	154 (138.12)	67 (82.88)	4.868	<0.05
E	2.2	157 (152.41)	7 (11.54)	1.9243	not signif.
	2.3	56 (53.62)	19 (21.38)	0.3705	not signif.
G	2.2 +2.3	144 (149.08)	36 (30.96)	0.9935	not signif.
T	2.3	107 (101.91)	17 (12.08)	2.3904	not signif.

expected results for the above two categories:

if P = frequency of browns eaten
and Q = " " greens "

(where $P+Q = 1$),

then the expected frequency of the sequences bb and gg is $(PP + QQ)$
and the expected frequency of the sequences bg and gb is $2PQ$ (where
b and g represent one eaten brown and one eaten green).

Table 40 gives the observed and expected results for each
bird in the two experiments. The data for C have again been
divided into his first 10 and last 6 days of predation.

Though only 1 of the 9 sets of data reveals significant
deviation in the direction predicted by searching images, 7 of
the 9 exhibit deviations in the direction expected. Furthermore,
the results taken as a whole indicate a significant tendency
for the colours to be taken in 'runs' $\left(\frac{(\chi)^2}{n} = 10.31, P < 0.01 \right)$,
implying that the birds were indeed tending to hunt by searching
image.

3. EXPERIMENT 2.3 (CONTD.). PARTS c, d AND e: TRIMORPHIC POPULATIONS

This short study was a prelude to those to be described in
the next Chapter. Its aim was to determine the responses of birds
to a third morph (khaki), when they were already familiar with
greens and browns. Since the new type of bait was intermediate
in colour between the standard greens and browns, the results
should provide a clue as to whether birds can discriminate between
such similar prey.

(a) Chronology

The dates (1968) of presentation were as follows:

Expt. 2.3 (cont.)

- c. From 4 February to 7 February: 90G + 20K + 90B
- d. From 8 February to 16 February: 67G + 67K + 67B
- e. On 17 February : 90G + 90K + 20B

In other words, the khakis were first introduced at relatively low frequency and this was increased during d and e.

(b) Materials and methods

The material for the new baits was made by thoroughly mixing equal amounts (by weight) of standard green and standard brown dough. After a uniform khaki colour had been attained the baits were manufactured in the same manner as described in Chapter III. These baits were also used in experiments described in Chapter IX. Plate 4 (page 199) shows the various shades of khaki that were used in these later experiments; the intermediate form (abbreviated to K in the Tables of the present Chapter) is labelled as '4'.

All the birds involved in 2.3a and b also preyed on the trimorphic populations, although E was absent during the duration of c. A new male blackbird (I) from an adjacent territory started to feed on the baits during the presentation of the 1:1:1 populations; in common with other intruders he was liable to attack from C and D.

(c) Results

(i) Summary of data

The complete daily record for the numbers of baits eaten and imprint-pecked is given in Table 43 page 196. Table 41 summarises

Table 41

Experiment 2.3 (cont.) c,d,e. Trimorphic populations (K=khaki) : grand totals of baits eaten and imprint pecked by blackbirds (C,D,E and I), robins, dunnocks and house sparrows. Expected predation, on the basis of the proportions offered is also shown.

[illegible]

these data and shows the overall results for imprint-pecking and predation by the five blackbirds and the robins, dunnocks and house sparrows.

(ii) Predation

The new morph clearly tended to be disregarded when first presented. Only the outsider, G, took khakis in any number. The other two blackbirds (for some reason E was absent during the whole of c.) concentrated on greens and browns, in particular the latter (favourite) variety. Robins and dunnocks also neglected khakis. The last species appeared to prefer greens; this belief is strengthened by the results for d. and e.

When the morphs were presented in equal frequencies blackbird D started to take khakis, and overall it took approximately equal proportions of the three morphs, though on a daily basis the results appear to be heterogeneous. G and E and the newcomer I tended to prey randomly. On the other hand, the three species of 'small' birds and blackbird C continued to neglect the khakis. The last bird was now concentrating almost entirely on browns.

Although fewer baits were taken, the trend observed in d. seems to be continued in e. That is, blackbirds D, E, G and I tended to predate in a random manner, whilst blackbird C, the robins, dunnocks and house sparrows tended to underpredate the khakis, which were now presented at a higher frequency than before.

4. DISCUSSION

This is an appropriate point to consider the behaviour of the two Turdus species when feeding on green and brown baits. The

discussion will also be concerned with the results described in the previous Chapter as well as those of the present one.

(a) Possible causes of brown preference

All three birds (A, B and T) in experiments 2.1a and 2.1b (Ch.VII) and four birds (C, D, T and G) in experiment 2.2 (this Ch.) took more browns than expected on the basis of random predation. One bird (E) took relatively too many greens in the latter experiment but in 2.3a this bird, as well as the other predators involved (C, D and G), preferred browns. In other words, six out of seven birds had preferences for browns and the seventh preferred browns one occasion and greens on another. This result reflects those given in Chapter VI where eleven experiments gave data for predation by groups of blackbirds and in every case browns were taken more often than expected assuming no selection.

The remainder of experiment 2.3 provides further evidence that blackbirds prefer brown to green. When a third, khaki, morph was presented in 2.3c, two of the blackbirds (C and D) took relatively more browns, whilst a third (G) took relatively more greens than expected. Khakis were almost completely neglected by C and D and were slightly overpredated by G. When the three colours were offered in equal frequencies in 2.3d, C was the only bird out of five that showed a distinct preference for brown: predation by the remaining birds was more or less random¹.

Chapter IX will also present evidence that blackbirds prefer brown to green. In the experiments described there, six out of

¹The data from 2.3c were too small to allow meaningful conclusions.

seven birds tended to take the browner varieties from a mixture of baits coloured various shades of green and brown. The seventh bird however showed a very definite predilection for certain types of green baits (see p. 228).

From the above we may conclude that most (though not all) blackbirds and songthrushes encountered preferred brown. This behaviour tended to persist within individuals (for four months, in the case of T; for eleven months, for C, D and G). It was recorded in both Edinburgh (Scotland) and Reading (England) separated by a distance of some 400 miles. In view of the consistency of these findings we should enquire into the causes of the colour preferences. There are five main possibilities.

(1) Relative conspicuousness

The experiments described in the last and the present Chapter were carried out on grass and it is conceivable that browns were preferred because they were relatively more conspicuous. To the human eye browns did appear to stand out more than greens, but not to such a degree as would be predicted by the results for songthrush T, for example. In addition, the other species (robins, dunnecks and house sparrows) in experiments 2.1, 2.2 and 2.3 had distinct preferences for green (see Tables IV and VIII, Allen 1967, for 2.1 and 2.2; Table 43, this thesis, for 2.3). If browns had appeared conspicuous to all birds then we would expect the last three species to also have chosen browns. Finally, similar experiments carried out on soil and snow backgrounds also revealed strong brown preferences in blackbirds and songthrushes (Ch. VI, p. 118). Taking all these facts into consideration we may conclude that the two species in question did not preferentially select browns because they

were more conspicuous than greens.

(ii) Taste

The results could of course be explained on the basis of differences in taste, but the evidence does not support this view. No great differences were detected in the high-density experiments described in Chapter IV: if anything, greens were preferred. Furthermore, some birds in the present experiments took browns to excess without ever sampling any greens. The most obvious cases concern blackbird A and songthrush T. Clearly these birds were not neglecting greens on the basis of taste; they did not take any greens at all during the greater part of 2.1.

(iii) Innate preferences

If the colour preferences were due to genetic causes then the situation would presumably be an example of behaviour polymorphism or 'polyethism' (Chance and Russell 1959). Various workers (e.g. Kear 1964, Weidmann 1965) have studied the colour preferences of new-born chicks of various birds but the individual responses appear to be relatively constant within species. It seems that the innate pecking responses of Turdus species have yet to be studied.

(iv) Permanent acquired preferences

Rabinowitch (1968) and others have shown that birds can acquire colour preferences through experience early in life (see p.36, this thesis). These preferences are rigid and permanent. It is well known that parent blackbirds feed their young with earthworms (Snow 1958) and is conceivable that the brown preferences are so acquired. Green preferences could be explained on the basis of early diets

containing a preponderance of green prey, for example, caterpillars.

(v) Temporary acquired preferences

The blackbirds and thrushes may have already been using searching images for brown prey prior to my experiments. Earthworms (Lumbricus spp. and Allolobophora spp.) were occasionally taken during the studies, sometimes in preference to baits. This was especially apparent at the start of experiment 2.2 and accounts for the low predation by the two birds involved. Perhaps significantly, they both took a majority of browns on these days.

Heppner (1965) has shown that Turdus migratorius hunts for the tips of earthworms in their burrows mainly on the basis of visual cues, probably shape or colour. If T.merula and T.philomelos also hunt earthworms in such a manner then they may well tend to attack brown objects within an area where they normally hunt earthworms. It should also be noted that the shape of a bait is not so far removed from that of the tip of an earthworm. Such a searching image may be 'area-associated' (Croze 1967, 1970), that is it may be restricted to sites where worms are found. In other areas the birds may switch to other searching images. For instance green searching images may be used when hunting in a tree which from past experience is associated with green caterpillars.

In the absence of appropriate behaviour experiments it is difficult to evaluate the causes of the preferences. Suffices it to say that in practice all five possibilities may be involved.

(b) Searching images

We must now examine the evidence that the birds were hunting by searching image. In particular, were the strong brown preferences

of T and A in the second part (b) of experiment 2.1 caused by the acquisition of searching images during the first part (a)? If this were the case then the preferences in 2.1b might be expected to have been stronger than the responses of naive birds to similar 9G:1B populations. Four such 'naive' birds were encountered: these were blackbirds C, D, E and G of experiment 2.2a. Thrush T in this experiment had already experienced baits in 2.1 and should strictly be neglected from the comparison, as should the Turdus individuals in 2.3 since these had all participated in 2.2.

In fact two of the four naive blackbirds in 2.2a took a clear majority of browns on the first day of predation, and these preferences were persistent. We have already mentioned that this behaviour may have been related to searching for earthworms. The preferences of these birds were not so strong as those of A and T in 2.1b. During the six days of 2.1b, A took 1 green and 130 browns and T took 0 greens and 176 browns. For the equivalent period at the start of 2.2, C and D took 17 greens, 75 browns and 56 greens, 31 browns respectively. This suggests that the preferences of A and T had been enhanced by brown-specific searching images. But in view of variability in behaviour, we must be wary of drawing a firm conclusion from these results. It is possible that A and T possessed strong brown preferences for reasons unconnected with conditioning to brown baits.

Additional support for searching images is that the birds were detecting the prey in 'runs' when they were feeding on 9:1 populations (the data from trimorphic populations were too scanty for meaningful analysis). These results suggest that the birds tended to search for one colour at a time and were capable of switching from using one searching image to using another; that is,

they 'switched attention' (cf. Dawkins 1971b). Similar results have been obtained by Pough (1964) for chickadees hunting dyed sunflower seeds and by Dawkins (1971b) for chicks feeding on orange and green grains of rice.

Croze (1967, 1970), on the other hand, found no evidence for 'runs' in crows preying on populations of red, black, and yellow mussel shells in equal proportions. He suggests that this inability to form searching images lowers the efficiency of the predator, for the crows took longer to find each prey in polymorphic populations than in equivalent monomorphic populations. This cannot be refuted by my work, since no monomorphic populations were presented and time measurements were not taken accurately; nevertheless the birds appeared to be hunting by searching image, for they were taking the baits in 'runs'.

Croze uses his data as support for 'adaptive polymorphism' (Dobzhansky 1951) which implies that polymorphic populations are more fit than those which are monomorphic. However the theory of adaptive polymorphism has yet to be substantiated: a polymorphism maintained by selection can occur in a population without affecting its adaptation (Cain and Sheppard 1954b). Croze's suggestion is nevertheless interesting and demands further investigation. But if colour polymorphism does increase protection from predation the question as to how it is maintained still remains unanswered. If predators are unable to form searching images then apostatic selection cannot be implicated.

(c) Relevance of imprint-picking

We noted that the onset of large-scale predation on a new colour is often associated with an increase in imprint-picking on

this colour. This was particularly noticeable for birds A and T in 2.1 but the birds of 2.2 also behaved in such a manner. It may follow that the strength of this type of imprint-pecking is directly proportional to the strength of the preference for the original colour, but the data are not conclusive.

L. Tinbergen (1960) and Mook et al. (1960) contended that a prey is not finally accepted until it has been subjected to frequent chance encounters. The increase in green imprint-pecks prior to the taking of greens supports this view of delayed acceptance, but indicates that the prey need not necessarily be eaten during this period. If the animal has a hard integument it may well survive imprint-pecking. Similar findings were made by Beukema (1968) when he introduced Drosophila larvae to sticklebacks accustomed to feeding on Tubifex worms. Results akin to mine were also reported by Harples (1933) in experiments designed to reveal the colour preferences of wild birds, notably tits (Parus major L. and P. caeruleus L.) and a nuthatch (Sitta europea L.). Coloured peanuts were presented in various proportions. Unfamiliarly coloured peanuts were pecked but not eaten at first and were taken only after repeated pecking.

Assuming that greens taste the same as browns, we must consider why they were often dropped after being picked up. Presumably the fact that they were the 'wrong colour' overrode any positive (or neutral) taste stimulus. A comparison can be drawn with the reactions of predators to Batesian mimics. Brower (1958, 1960) has shown that an avian predator familiar with a distasteful model may sometimes accidentally pick up a mimic, but release it again. In this situation the predator belatedly

'realises' that the prey is the 'wrong colour' even though it is not distasteful. But the 'wrong colour' is the familiar one. Such findings were obtained for Scrub Jays (Cynocitta caerulea) feeding on mimetic butterflies (Brower 1958) and for starlings (Sturnus vulgaris) feeding on mealworm 'models' and 'minics' (Brower 1960). In Batesian mimicry a rare palatable prey species is protected by resembling a common distasteful prey species; in non-mimetic colour polymorphism a rare palatable morph may gain protection by virtue of it being different from a common variety. In each case an accidental attack on the rare type need not necessarily result in its death.

Imprint-pecking was not limited to the occasions mentioned above; both colours tended to be imprint-pecked (at random?) at other times in the experiments. Sometimes the cause was recognisable, for example; a sudden fright at the moment when the bird was picking up a bait, but in most cases the cause was not obvious.

(d) Diversity of behaviour and its implications

(1) Diversity of behaviour

The birds clearly differed in their overall responses to the baits. The strengths of their preferences ranged from T's almost total preoccupation with browns to the more random predation of E. Other forms of behaviour also revealed idiosyncrasies, for example, with regard to the imprint-pecking (e.g. the behaviour of birds prior to the acceptance of novel baits, p.157f. and p.170ff; the excessive imprint-pecking by C, p.170 ; the unusual form of imprint-pecking exhibited by A and T, p.158). Indeed my long periods of observation soon convinced me that each bird had a

'character of its own'. The recognition of these idiosyncrasies was partly based on subjective impressions. Thus G¹ was by far the least afraid of man, while B was the most timid.

Other differences were potentially measurable but had to be neglected because of the difficulties of attempting to observe many things at one time (see p. 60). One example is the speed at which the baits were eaten. The territorial 'owners' of the plots (blackbirds A and B in 2.1; C and D in 2.2 and 2.3) tended to chase out intruding blackbirds and songthrushes, and these interlopers thus tried to grab as many baits as quickly as possible. Blackbirds G, I and to a lesser extent, E, were such birds. It may be significant (although the sample is small) that these birds tended to be the least selective; with such a premium on the baits, their preferences were relinquished. The 'resident' birds on the other hand had more time to exercise their choice. The behaviour of songthrush T does not fit the above argument because this bird was almost invariably attacked when in the plot and yet was the most selective. Do intra- and inter-specific competition have different effects on prey selection?

The heterogeneity of behaviour was probably caused by a combination of both genetic and environmental factors. The overall proportions taken by a given bird were no doubt influenced by the strength of its colour-preference. In other words the causes of the diversity of response may be identical to the causes of the colour preferences which were discussed in (a). It is also likely that a bird's first (chance?) encounters with the baits influenced its subsequent selection (cf. Tinbergen 1960). We have seen that this certainly

¹This bird had the audacity to beg for (toast-coloured) crumbs at the breakfast table!

seems to have been the case for A and T in experiment 2.1a. These birds apparently acquired searching images for brown baits in addition to their natural brown preferences.

Variation between the responses of individual predators has been reported by other workers, for example with regard to unpalatable prey. Thus Cott (1940, p.286) writes: "individual toads appear to differ widely in intelligence and rate of learning" in response to warningly coloured bees. Comparable results have been obtained for palatable prey and were discussed in Chapter II. Smith (1967) with sticklebacks and Pough (1964) with chickadees, both produced similar results for predators feeding on artificial prey. More recently Mrs. Pat Miller (thesis in preparation) has detected great variability between individual quails feeding on artificial prey. We should also not overlook L. Tinbergen's (1960) original discovery of the diversity in the responses of individual tits hunting for insects in pine forests.

On the other hand, the three rudd used in the experiments of Popham (1941, 1942) appeared to show almost identical responses to corixid bugs (Elton and Greenwood 1970). However this result is not necessarily contradictory to those mentioned above. The three fish might have been taken from a population showing great behaviour variability and their apparent uniformity could have been a result of chance errors in sampling. A repetition of Popham's experiments would be a worthwhile investigation.

(ii) Apostatic selection

We have seen that some Turdus individuals took browns alone, whether they were presented with 9G:1B or 1G:9B populations. Such behaviour is of course not predicted by the hypothesis of apostatic selection. When selection by groups of birds was examined, however,

we found that the combined effect was apparently frequency-dependent, assuming constant selection, in 13 out of 14 '9:1' experiments (Chapter VI). On average, individual birds tended to hunt for the commoner colours.

There may be two main reasons for the disparity between the findings for individual birds (Chapters VII and VIII) and groups of birds (Chapter VI). First, birds such as A and T, with very strong brown preferences may have been in the minority in each of the 13 experiments with the result that their effect was overruled by the frequency-dependent tendencies of other individuals. Second, those birds which did start by taking the rare colours alone may have found this behaviour unprofitable and switched to searching for the common varieties. One factor which may aid this change is social facilitation.

Various workers have shown that some animals can learn from the experience of others and this has been termed 'observational learning' (for a source of references to the psychological literature, see John et al. 1968). Birds have often been shown to learn from watching others during feeding; examples of species that have been investigated are: Chloris chloris, Klopfer 1961; various Fringidae, Kear, 1962; Passer domesticus and Fringilla coelebs, Turner 1965; domestic chicks, Tolman 1968; Columba palumbus, Hurton 1971b). These birds feed in dense flocks and it has been suggested that communal feeding and roosting improve the feeding prospects of the individual (Ward 1965, Zahavi 1971, Hurton 1971a). In view of this evidence we might predict that social predators hunting for rare prey items may lose their searching images in preference for more profitable ones by watching and

copying the behaviour of others. Apparently just this has been recently demonstrated by Murton (1971b) for woodpigeons Columba palumbus feeding on seeds¹.

There is no conclusive direct evidence that social facilitation contributed to the overall frequency-dependent results of my 9:1 experiments. In experiment 2.1b for example, blackbird B took greens whilst her mate A continued searching for rare browns, even though the birds were often in the plot together. In experiment 2.2, blackbird D took a majority of rare browns on the first day and on subsequent days tended to concentrate on greens, while his mate blackbird C gradually changed to accepting greens throughout the period of study. There is no clear evidence that the alterations in the behaviour of either of these birds was related to social facilitation between them. An important consideration is that the blackbirds did not appear to be particularly 'social' feeders. Even when both resident birds (A and B in 2.1, C and D in 2.2 and 2.3) were in the plot they kept very much to themselves and often fed in different areas.

The fact remains that most of the 9:1 experiments gave indications of frequency-dependent selection for predation by wild passerines en masse. In some experiments (1, 3.1, 3.3, 3.4, 4) large numbers of birds of various species were involved and it is possible that social facilitation helped to ensure that the birds hunted on average for the commoner colours. In each of the other experiments (3.2, 5.1, 5.2, 5.3, 5.4, 5.5, 6.1, 6.2) less than six predators were involved, sometimes only two (experiments 5.3 and 5.4).

¹Murton's (1971b) paper had not been read at time of writing. It is quoted in his (1971a) article.

Yet the apostatic effects of the predation in the last group of experiments seem to be no less marked than those of the first (Tables 19 and 20, pages 114, 115). The possibility that Turdus individuals learn from others that certain prey are more profitable has yet to be substantiated.

Social facilitation is potentially an important tool for strengthening apostatic selection and some polymorphic species undoubtedly fall prey to birds feeding in flocks. But what of songthrushes and Cepaea, for example? The songthrush is usually an unsocial bird in the British Isles and is unlikely to hunt Cepaea in dense flocks. In this situation it is improbable that songthrushes acquire profitable searching images by direct observation of other individuals. However, there remains one other possibility. Although songthrushes may search for snails independently of one another, they may tend to break the shells at a common site, particularly if few anvils are available (Morris 1954). A thrush with an unprofitable searching image may be able to form a new one on the basis of the shell remnants at the anvil. If this were true it would be an indirect form of social facilitation. This hypothesis may not be so fanciful as it may seem; songthrushes are known to respond to empty snail shells (Morris op.cit.) and it is the colour and pattern of the pieces that would be important, not their irregular, non-snail-like shape (p. 37).

(iii) Predators and area effects

In (i) we remarked that the results may suggest that blackbirds are more selective within their territories. Since the data also show that individual birds vary considerably in their preferences it

follows that pairs of birds may also differ in their overall responses. L. Tinbergen (1960) in fact demonstrated that pairs of tits in adjoining territories show different preferences for insect species. In view of this the morph frequencies of a polymorphic prey species might be markedly different in adjoining territories even when there are no apparent differences between the habitats. The degree of permanence of such areal differences would then depend largely on the permanence of the territories. Thus since songthrush pairs tend to keep the same territories for a year and sometimes longer (Davies and Snow 1965) we may predict that discontinuities of morph-frequency in Cepaea could last for a similar duration. To my knowledge no one has attempted to find any relationship between morph-frequencies in Cepaea and territories of songthrushes.

Croze (1967) has extended this argument in an attempt to provide an explanation for 'area effects' in Cepaea as first detected by Cain and Currey (1963) and later confirmed by other workers (e.g. Carter 1968, Arnold 1971 for Cepaea; Clarke 1968 for Partula taeniata). Area effects are characterised by areas of constant morph frequencies which may change within distances of 200 m or less without reference to the environment. They may extend for 10 sq. km or more. Croze (1967) suggests that they may be the result of area-restricted predation by certain species with large hunting areas. Songthrushes are ruled out because of their relatively small territories and Croze suggests Corvidae as the most likely candidates. He admits that his is 'gross speculation' and the long existence (from at least the Neolithic, Cain and Currey 1963) of area effects argues against this explanation.

A more likely hypothesis based on selective predation is that area effects are associated with the distribution of a particular species of predator (Cain and Currey 1963, Croze 1967, O'Donald 1968).

No such correlations have yet been detected, but if it is true that songthrushes, like blackbirds, prefer browns (and the evidence from Chapters VII and IX implies that they do) then this species may be implicated. Some area-effects in Cepaea are characterised by high frequencies of brown morphs (Cain and Currey, op.cit.). Perhaps such localities are correlated with the absence or near-absence of songthrushes.

Of course, at this stage we know little of the colour preferences of songthrushes in nature. Is the preference for brown widespread geographically? Even if it is we cannot eliminate the possibility that yellow, for example, is preferred to brown, for the types of colours used in my experiments were strictly limited.

In fact, the preferences of songthrushes might well vary from place to place, perhaps depending on the colour and abundance of alternative prey (p. 181). This leads to another possible explanation for area effects¹. In places where earthworms are common thrushes might be expected to take relatively too many brown morphs if Cepaea is present. Where there is an abundance of palatable yellow (or even green) caterpillars the birds may tend to overpredate the yellow morphs. Distasteful prey might also affect morph frequencies in Cepaea. Thrushes which have experienced aposematic yellow-and-black striped prey may be prone to avoid yellow effectively banded Cepaea.

It follows that area effects in Cepaea might be related to the distribution of other prey species which contribute to the diets of its major predators, bearing in mind that the songthrush is not the

¹I am grateful to Professor B.C.Clarke for drawing my attention to this hypothesis.

only predator of Cepaea. Although Cain and Currey (1963) were unable to detect any obvious relationships between area effects and the distribution of other species the situation warrants a larger ecological survey than they were able to carry out.

(e) Introduction of third morph

The results of 2.3 c, d, e support many of the findings from the dimorphic 9:1 experiments. The birds were again shown to be diverse in their responses. Equally important, the khaki morph was found to have an overall advantage when first introduced. This suggests that the birds had become accustomed to searching for greens and browns and overlooked the novel prey. If so, then this would be further evidence for apostatic selection. However, the data do not exclude the possibility that khaki was neglected because of some factor independent of searching images. Further experiments with khaki morphs were deemed necessary.

5. SUMMARY OF CONCLUSIONS FROM EXPERIMENTS IN CHAPTERS
VII AND VIII

Data were obtained for the individual responses of blackbirds and a songthrush. In summary, the main conclusions were:

- (a) Most of the birds had frequency-dependent preferences for browns.
- (b) One blackbird selected in an apostatic manner.
- (c) Large-scale predation on an unfamiliar colour was preceded by an increase in the frequency of 'imprint-pecking'.
- (d) The birds differed markedly in their responses to the baits and in other aspects of behaviour.
- (e) There was evidence that the birds were hunting by searching image.

APPENDIX C: TABLES 42 AND 43

Full results for experiments 2.2 and 2.3, Chapter VIII

Table 42

Experiment 2.2. Full daily results for blackbirds C, D, E, G and songthrush T. Imprint-pecked baits are shown in parentheses. The numbers of visits (v) per day are also given.

180 greens + 20 browns

Date (1967)	B L A C K B I R D S												THRUSH		
	C			D			E			G			T		
	G	B	v	G	B	v	G	B	v	G	B	v	G	B	v
20.3	(4) + 3	(2) + 9	8	1 (1) + 7	5		-	-		-	-		-	-	
21.3	(2) + 1	(3) + 18	17	(5) + 14 (1) + 4	12		-	-		-	-		-	-	
22.3	(4) + 1	(14) + 15	19	(8) + 15 5	14		-	-		-	-		-	-	
23.3	(9) + 4	(20) + 16	20	(1) + 9 (1) + 5	13		1	0	1	-	-		-	-	
24.3	(9) + 2	(23) + 11	17	(1) + 7 7	10		(4) + 4	0	5	-	-		-	-	
25.3	(16) + 6	(6) + 6	11	(1) + 10 3	9		(3) + 12	0	8	-	-		0	8	
26.3	(6) + 2	(28) + 9	11	(3) + 11 3	11		(2) + 24	0	8	-	-		0 (1) + 14		
27.3	(18) + 3	(17) + 8	11	(1) + 14 4	11		(3) + 18	0	10	-	-		(2) + 0 16		
28.3	(22) + 5	(16) + 8	15	(2) + 11 (1) + 3	14		(7) + 22 (1) + 0	11		-	-		0 17		
29.3	(22) + 14	(6) + 3	14	(3) + 10 2	10		(3) + 17	0	7	0	(2) + 0	1	0 17		
30.3	(32) + 16	(3) + 2	16	(1) + 6 8	12		(5) + 16	0	9	-	-		0 11		
31.3	(18) + 15	(11) + 2	12	(2) + 14 (1) + 3	12		(4) + 13	0	6	-	-		(3) + 2 4		
1.4	(11) + 16	(2) + 3	17	(2) + 10 2	9		17	0	7	0	1	1	(1) + 3 16		
2.4	(7) + 3		5	-	-		5	1	2	(1) + 4	1	3	-	-	
3.4	(4) + 6		10	8	1	5	(1) + 9	5	6	20	3	8	2	14	
Grand totals	97 (184)	113 (151)	202	140 (30)	57 (5)	147	158 (32)	6 (1)	80	24 (1)	5 (2)	13	7 (6)	117 (1)	59

* One of these baits was imprint-pecked in an abnormal manner (see p.158).

Table 43 Experiment 2.3. Full daily results for blackbirds C, D, E, G, I and robins (2 individuals?), dunnocks (4?) and housesparrow (4?). Inprint-pecked baits are shown in parentheses and the numbers of visits per day are also given.																																	
	Date (1968)	C			D			E			G			I			ROBINS			DUNNOCKS			HOUSE-SPARROWS										
		G	B	v	G	B	v	G	B	v	G	B	v	G	B	v	G	B	v	G	B	v	G	B	v								
a. 180 greens + 20 browns	16.1	-	-	-	(1) 16	-	2	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
	17.1	-	-	-	(3) 19	-	1	13	-	-	-	(3) 12	-	2	5	-	-	-	-	-	-	-	-	-	-								
	18.1	-	-	-	16	(1)	4	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
	19.1	-	-	-	8	(1)	2	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-								
	20.1	-	-	-	6	-	3	7	2	(1)	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-								
	21.1	-	-	-	10	-	2	6	(2) 11	-	0	6	(3) 8	(1)	0	4	-	-	-	-	-	-	-	-	-	-							
	22.1	-	-	-	10	(1)	5	11	12	-	2	6	10	(1)	2	5	-	-	-	-	-	-	-	-	-								
	23.1	(9) 9	(2)	4	9	14	-	6	14	(1) 11	-	0	5	14	(1)	3	7	-	-	-	-	-	-	-	-	-							
	24.1	(7) 11	(2)	1	7	(2) 6	-	10	12	6	-	3	3	(1) 21	(1)	0	7	-	-	-	-	-	-	-	-	-							
	25.1	(6) 18	-	0	9	(2) 7	-	9	13	4	-	0	2	14	-	1	4	-	-	-	-	-	-	-	-	-							
	26.1	(3) 15	-	1	6	11	-	3	9	8	-	3	4	12	-	2	4	-	-	-	-	-	-	-	-	-							
	27.1	(5) 8	-	6	8	6	-	5	8	3	-	1	2	6	-	1	2	-	-	-	-	-	-	-	-	-							
	28.1	(6) 11	(2)	2	8	(1) 13	(2)	1	10	1	-	0	1	15	-	1	5	3	0	3	-	-	-	-	-	-							
	29.1	(6) 8	(6)	3	9	(1) 13	-	2	9	5	-	4	3	11	-	1	5	3	0	3	1	0	1	3	0	3							
	30.1	(4) 8	(6)	2	10	13	-	3	13	7	-	0	3	13	-	0	3	5	0	5	9	0	9	2	0	2							
	31.1	(12) 13	(3)	2	13	10	(1)	1	10	2	-	0	2	15	-	1	6	5	0	5	9	0	9	-	-	-							
Grand totals		(58) 101	(19) 21	79	(10) 178	(6) 59	167	(3) 72	(1) 15	40	(7) 155	(4) 16	60				15	0	16	20	0	20	5	0	5								
b. 20 greens + 180 browns	1.2	(3) 0	(9) 8	9	0	-	16	10	1	-	10	2	2	-	16	7	0	1	1	3	1	4	-	-	-								
	1.2	0	(13) 13	8	1	-	11	8	0	-	6	2	2	-	27	7	0	5	5	3	8	11	-	-	-								
	Grand totals	(3) 0	(22) 21	17	1	-	27	18	1	-	16	4	4	-	43	14		0	6	6	6	9	15	-	-	-							
c. 90 greens + 90 browns + 20 khakis	4.2	3	0	(2) 6	3	3	0	10	6	-	-	-	-	-	-	-	-	-	-	1	0	4	3	1	1	1	13	-	-	-	-		
	5.2	(4) 2	0	(24) 17	12	5	0	18	14	-	-	-	-	7	1	0	2	-	-	2	0	8	10	15	0	2	17	-	-	-	-		
	6.2	(2) 5	0	(7) 16	11	5	1	15	12	-	-	-	-	11	2	4	4	-	-	5	0	3	8	11	0	1	12	-	-	-	-		
	7.2	(3) 3	0	(18) 15	16	(1) 4	0	14	11	-	-	-	-	19	4	7	5	-	-	7	0	3	10	4	0	3	7	-	-	-	-		
	Grand totals	(9) 13	0	(51) 54	42	(1) 17	1	57	43	-	-	-	-	37	7	11	11	-	-	15	0	18	31	31	1	7	39	-	-	-	-		
d. 67 greens + 67 browns + 67 khakis	8.2	(1) 0	0	(10) 17	8	2	3	10	8	1	1	1	1	8	7	8	6	-	-	3	1	8	12	8	0	4	11	-	-	-	-		
	12.2	0	0	(17) 14	7	8	5	1	6	-	-	-	-	2	1	1	1	-	-	3	0	6	9	7	2	4	13	-	-	-	-		
	13.2	1	(2) 1	(32) 14	8	(1) 6	6	2	8	0	0	(1) 1	1	2	2	3	2	-	-	4	1	7	12	7	0	3	10	6	0	2	8		
	14.2	0	0	(12) 16	10	6	(1) 8	3	8	2	1	2	2	3	6	5	5	-	-	5	2	5	12	7	1	4	12	-	-	-	-		
	15.2	0	0	(12) 11	7	3	0	10	7	1	2	3	3	7	9	(1) 6	7	2	6	6	6	6	7	9	1	9	19	3	0	1	4		
	16.2	0	0	(12) 16	11	(1) 8	(1) 3	(1) 4	7	1	2	0	4	9	4	6	5	0	9	7	5	4	2	1	7	10	2	5	17	3	0	0	3
	Grand totals	(1) 1	(2) 1	(95) 88	51	(2) 33	(2) 25	(1) 30	44	5	6	(1) 7	11	31	29	29		2	15	13	11	23	7	29	59	48	6	29	82	12	0	3	15
e. 90 greens + 20 browns + 90 khakis	17.2	(5) 14	0	(2) 0	8	9	(1) 4	0	7	3	3	1	7	6	8	1	4	9	7	2	7	6	2	1	9	13	1	1	15	2	0	0	2

Table 43 Experiment 2.3. Full daily results for blackbirds C, D, E, G, I and robins (2 individuals?), dunnocks (4?) and housesparrows (4?). Inprint-pecked baits are shown in parentheses and the numbers of visits per day are also given.

CHAPTER IX FURTHER EXPERIMENTS WITH GREENS, BROWNS AND
INTERMEDIATE COLOURS

CHAPTER IX FURTHER EXPERIMENTS WITH GREENS, BROWNS AND
INTERMEDIATE COLOURS

1. INTRODUCTION

The results of the last experiment of the previous Chapter showed that a third, khaki, prey can be overlooked by predators. In this Chapter we examine further studies involving baits of various shades of khaki.

The work was divided into two parts. In the first, an attempt was made to determine the specificity of searching images. The experiments of Chapter V clearly showed that wild birds can discriminate between standard greens and browns after appropriate training. But as pointed out at the time, polymorphs of natural prey are often much more visually similar than the standard dimorphs used in my experiments. In the work to be described, this discrepancy was rectified by giving birds the opportunity of discriminating between baits of relatively greater visual similarity than standard greens and standard browns.

If colour polymorphisms are in fact maintained by apostatic selection then how did they originally evolve? The second set of experiments examines the possibility that predators are capable not only of maintaining, but also of promoting polymorphisms in their prey by exercising disruptive selection. Consider the hypothetical evolution of polymorphism within a 'species' of bait that exhibits continuous variation in colour ranging from brown to green. This variation is distributed normally around a mean colour composed of brown and green in equal proportions. Ideally we should present such populations to wild birds. Observations of the response of



Plate 4

Appearances of the nine morphs as used
in experiments described in Chapter IX.
Increasing greenness from left to right.
The baits are each 0.7 cm long.

the population to selection should determine whether discontinuous variation is evolving. This could occur if, for instance, the predators concentrate on searching for the commonest colours. Such behaviour would imply the existence of searching images of a highly specific nature.

Two experiments were carried out along the above lines. In practice it was necessary to limit the number of types of baits. Nine varieties were offered and it may therefore be argued that the populations were already polymorphic. Even so, I often had difficulty in distinguishing between the different shades of khaki.

The two groups of experiments are first described separately. They are then collated in a general discussion and are compared with other researches, particularly those of Croze (1967, 1970). The khaki colour-types were basic to all the experiments and are dealt with below.

2. PREY

The nine varieties of bait are shown in Plate 4. Table 44 gives details of their optical properties. Each morph is numbered according to its difference from standard brown in arbitrary units. Thus 0 represents the base colour; 4, the intermediate khaki as used in experiment 2.3, Chapter VIII; and 8, standard green.

The baits were made by mixing standard green and standard brown dough (see page 55) in the appropriate proportions by weight. For example, 4's contained equal quantities of green and brown dough, whilst 7's were made from seven parts of green to one of brown. Large numbers of baits were made at the same time and their method of manufacture was as described in Chapter III. The non-chromatic

Table 44

Colours of the nine green, khaki and brown baits used in experiments described in Chapter IX. The data were determined by use of the Munsell Book of Color (1966). I am grateful to Professor Bryan Clarke of the Genetics Department, University of Nottingham for supplying these data.

Colour of bait	Hue	Value/chroma
<u>0</u> (standard brown)	5 YR	6/6
<u>1</u>	7.5 YR	7/6
<u>2</u>	10 YR	6/4
<u>3</u>	2.5 YR	6/4
<u>4</u>	5 Y	7/4
<u>5</u>	10 Y	6/4
<u>6</u>	2.5 GY	6/4
<u>7</u>	5 GY	6/6
<u>8</u> (standard green)	7.5 GY	7/10

Note: The hue of a colour indicates its relation to red, yellow, green, blue and purple; the value its relative lightness or gray value; and the chroma its strength.

properties of the baits were kept as constant as possible and were no different from those of the standard greens and browns used in previous experiments.

3. EXPERIMENTS 1 AND 2: TRAINING

(a) Introductory remarks

These experiments were similar in design to those described in Chapter V; birds were first trained on one colour and then presented with 1:1 populations. The most important difference was that the baits employed in each experiment were visually more similar.

(b) Plan

Four experiments were carried out and all involved initial training sessions with 4's. They were divided into two separate series which were planned as follows:

Series 1 (July 1969) comprised two experiments at separate sites. After being trained on 4's, the birds were presented with 1:1 populations. In one experiment these populations contained 4's and 8's (standard greens). At this site the birds were next trained on 8's and then offered 1:1 populations as before. The second experiment was of similar design, except that 0's (standard browns) were used in place of 8's.

Series 2 (August-September 1969) also involved two experiments at different locations. They differed from those of series 1 in that the baits were visually more similar. In addition to 4's, one experiment incorporated the presentation of 2's, whilst the

Table 45

Sites of specificity training experiments, giving O.S. grid references.

All experiments were carried out on short grass.

Expt.	Site
1.1	Lawn in front of Zoology Department, Kings Buildings, Edinburgh. N.S. 268707
1.2	Golf course near the Poultry Research Centre, Kings, Buildings. N.S. 263705
2.1	Lawn in front of Chemistry Department, Kings Buildings. N.S. 266707
2.2	Playing fields, Liberton Dams. N.T. 272704

Table 46

Dates of training and presentation of 1:1 populations in experiments of series 1 and 2. All dates are inclusive.

Expt.	Colours	TRAINING ON 4's		REVERSAL-TRAINING	
		Dates of training (1969)	Dates of presentation of 1:1 pops.	Dates of training (1969)	Dates of presentation of 1:1 pops.
1.1	<u>4</u> & <u>8</u>	5.7 - 12.7	13.7 - 15.7	17.7 - 23.7	24.7 - 25.7
1.2	<u>4</u> & <u>0</u>	5.7 - 12.7	13.7 - 16.7	17.7 - 23.7	24.7 - 25.7
2.1	<u>4</u> & <u>6</u>	18.8 - 24.8	25.8 - 27.8	28.8 - 3.9	4.9 - 5.9
2.2	<u>4</u> & <u>2</u>	18.8 - 24.8	25.8 - 27.8	28.8 - 3.9	4.9 - 5.9

other employed 6's.

Thus each experiment consisted of two parts: a. training with 4's, followed by presentation of 1:1 populations; b. reversal-training and presentation of 1:1 populations.

(c) Materials and methods

(i) Locations

All four experiments took place on short grass at different sites within a $\frac{1}{2}$ -mile radius of the Department of Zoology, University of Edinburgh (see Table 45). Each experimental plot was a square consisting of twenty-five metre-squares.

(ii) Procedures

Table 46 gives the dates of the periods of familiarization and presentation of 1:1 populations. The training sessions all lasted for one week and approximately 2,000 baits were consumed at each site. Populations containing 25 of each of the relevant colours were presented during the first two or three days following the ends of the training sessions. They were observed continuously and were maintained in the usual manner, with frequent replacement of eaten baits. The times of presentation of 1:1 populations are given with the results in Tables 48a and 48b.

(iii) Predators

Blackbirds preyed on the baits in all four experiments. In addition house sparrows and dunnecks were involved in experiments 1.1 and 2.1 and the predation effected by these 'small' birds was calculated in the usual fashion (see p. 85). Estimates of the numbers of birds involved are given in Table 47.

Table 47

Grand totals of baits taken from 1:1 populations after training, by blackbirds (Bl) alone or with house sparrows (HS) and dunnocks (D). The estimated numbers of each species involved are given in parentheses.

	Expt. 1.2 Bl (3)	Expt. 2.2 Bl (4)	Expt. 2.1 Bl (4) + HS (6) + D (2)	Expt. 1.1 Bl (5) + HS (6) + D (2)
	<u>4</u> <u>0</u>	<u>4</u> <u>2</u>	<u>4</u> <u>6</u>	<u>4</u> <u>8</u>
a. AFTER TRAINING ON 4's				
Grand totals	80 61	101 78	96 77	128 59
$\chi^2_{(1)} \text{ (deviation from 1:1)}$ P	2.560 N.S.	2.688 N.S.	2.087 N.S.	25.460 0.001
b. AFTER REVERSAL-TRAINING				
Grand totals	45 62	52 68	59 77	64 74
$\chi^2_{(1)} \text{ (deviation from 1:1)}$ P	2.701 N.S.	2.133 N.S.	2.382 N.S.	0.725 N.S.
$\chi^2_{(1)} \text{ (heterogeneity between grand totals)}$ P	5.245 <0.05	4.927 <0.05	4.466 <0.05	16.001 <0.001

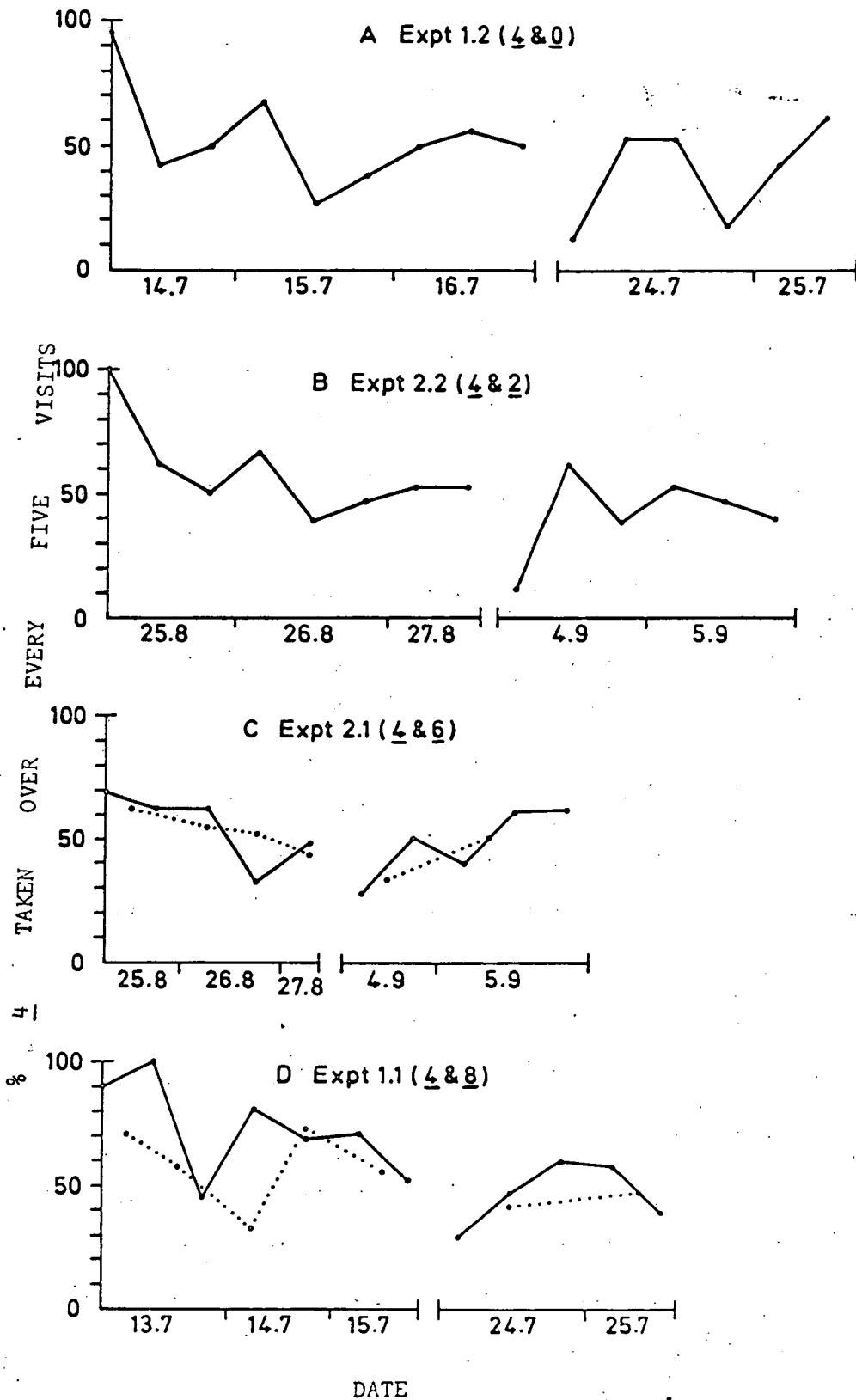
(d) Results

Tables 48a and 48b (pages 209 and 210) give the results for daily predation on populations presented in series 1 and 2 respectively. Analysis by chi-squared shows that the proportions taken per day do not differ significantly within parts a. and b. of each experiment. These data have therefore been pooled and are given in Table 47. This Table does not present the experiments in chronological order (from left to right), but in a sequence according to the relative greenness of the baits that were offered with the 4's. Furthermore, the results for predation by blackbirds and 'small' birds in experiments 1.1a, 1.1b and 2.1a, 2.1b have also been amalgamated. This seems a legitimate procedure because there is no significant heterogeneity in the overall proportions taken by the two groups of birds within the halves of the relevant experiments (see Tables 48a and 48b).

There can be no doubt as to the effects of training. Direct comparison between the two grand totals for each experiment reveals that the proportions differ significantly in every case (bottom row, Table 47). Moreover, all eight grand totals deviate from 1:1 in the directions expected on the basis of conditioning. The results for experiment 1.1a, however, are the only data that differ significantly from the expected ratio.

Further evidence for conditioning can be obtained by examining the data in greater detail. The graphs shown in Fig. 11 illustrate the relationships between the percentages of 4's taken over every five visits. Since the numbers of predated baits were small these percentages are subject to sampling error. In spite of this, the graphs have striking similarities.

Figure 11



Percentage of 4's taken over every 5 visits from 1:1 populations after training in experiments 1.2 (blackbirds), 2.2 (blackbirds), 2.1 (blackbirds, house sparrows, dunnocks), 1.1 (blackbirds, house sparrows, dunnocks). Besides 4's the experiments involved 0's, 2's, 6's and 8's respectively.

The highest percentages of 4's were generally taken immediately after the first training periods. This is especially true for predation by blackbirds in 1.2a, 2.2 and 1.1. The blackbird and small bird results for 2.1 also fit this generalization, though the effects are not as pronounced. These results are mirrored by those for the second parts of the experiments. All the birds began by taking relatively low proportions of 4's; that is, they continued to search for the familiar colours. This may imply that the tendency to take the conditioned colour declined with time (as was noted in experiments described in Chapter V) but in fact none of the data exhibited significant decreases in the proportions taken over every five visits (Spearman's rank correlation test).

4. EXPERIMENTS 3 AND 4: 'NORMALLY-DISTRIBUTED' POPULATIONS

(a) Introductory remarks

The training experiments demonstrated that birds can distinguish between baits of similar colour and these findings stimulated the inception of the two investigations described below. The first experiment (experiment 3¹) was essentially a short pilot study designed to test the method. Experiment 4¹ was a more prolonged investigation.

As will be seen, the principle aim of the work was to detect changes in the structures of the populations resulting from selection by predators en masse. Nevertheless it was possible, especially in the second experiment, to record the behaviour of individual *Turdidae*.

¹The experiments are numbered in sequence with the two series of training experiments.

Table 48a

Specificity training experiments: series 1. Daily results for predation by blackbirds (Bl) and small birds (S), i.e. house sparrows and dunnocks.

<u>Experiment 1.1</u>					<u>Experiment 1.2</u>				
Date	Times of observations (B.S.T.)	Predation			Dates	Times of observations (B.S.T.)	Predation		
		Bl	S				Bl		
		<u>4</u>	<u>8</u>	<u>4</u> <u>8</u>			<u>4</u>	<u>0</u>	
a. AFTER TRAINING ON <u>4</u> 's									
13.7	1405-1730	34	8	24	10	14.7	1240-1645	31	17
14.7	1900-2040	22	7	12	11	15.7	1311-1430	26	23
15.7	1925-2050	22	13	13	10	16.7	1300-1642	23	21
Grand totals		79	28	49	31	Grand totals		80	61
$\chi^2_{(2)}$	(het. between days)	3.005	2.263		$\chi^2_{(2)}$	(het. between days)	1.831		
		(N.S.)	(N.S.)				(N.S.)		
$\chi^2_{(1)}$	(het. between G.T.'s)	3.355							
		(N.S.)							
b. AFTER REVERSAL TRAINING									
24.7	1930-2140	26	30	10	14	24.7	1020-1215	8	20
25.7	1951-2130	19	20	9	10	"	1410-1645	16	21
						25.7	0950-1415	21	21
Grand totals		45	50	19	24	Grand totals		45	62
$\chi^2_{(1)}$	(het. between days)	0.048	0.139		$\chi^2_{(2)}$	(het. between trials)	3.198		
		(N.S.)	(N.S.)				(N.S.)		
$\chi^2_{(1)}$	(het. between G.T.'s)	0.121							
		(N.S.)							

Table 48b

Specificity training experiments: series 2. Daily results for predation by blackbirds (Bl) and small birds (S), i.e. house sparrows and dunnocks.

<u>Experiment 2.1</u>					<u>Experiment 2.2</u>				
Date	Times of observations (B.S.T.)	Predation				Date	Times of observation (B.S.T.)	Predation	
		Bl	S					Bl	
		<u>4</u>	<u>6</u>	<u>4</u>	<u>6</u>			<u>4</u>	<u>2</u>
a. AFTER TRAINING ON <u>4</u> 's									
25.8	1930-2140	21	11	12	7	25.8	1059-1715	37	18
26.8	1650-2106	23	19	19	16	26.8	1021-1521	31	30
27.8	1920-2146	14	15	7	9	27.8	1000-1530	33	30
Grand totals		58	45	38	32	Grand totals		101	78
$\chi^2_{(2)}$ (het. between days)		1.930	1.318			$\chi^2_{(2)}$ (het. between days)		3.830	
		(N.S.)	(N.S.)					(N.S.)	
$\chi^2_{(1)}$ (het. between G.T.'s)		0.069							
		(N.S.)							
b. AFTER REVERSAL TRAINING									
4.9	1850-2131	19	29	7	16	4.9	1100-1630	24	37
5.9	1708-2101	21	20	12	12	5.9	1005-1650	28	31
Grand totals		40	49	19	28	Grand totals		52	68
$\chi^2_{(1)}$ (het. between days)		1.209	1.867			$\chi^2_{(1)}$ (het. between days)		0.804	
		(N.S.)	(N.S.)					(N.S.)	
$\chi^2_{(1)}$ (het. between G.T.'s)		0.256							
		(N.S.)							

(b) Basic design of experiments

The second experiment differed from the first in that it was preceded by a period of training with 4's. The reason for this will become clear later. In other respects, however, the two studies were essentially similar in design.

(i) Prey

Nine morphs were used. These ranged in colour from 0 (standard brown) to 8 (standard green) and are illustrated in Plate 4, page 199.

(ii) Presentation of populations

Birds were first offered populations with the morphs in frequencies that approximated to the normal distribution (see Table 49). The frequencies of the two extreme colours were correlated with the tails of the distribution, whilst 4's constituted the mean (and mode).

Table 49

Initial composition of 'normally-distributed' populations expressed in percentages.

Morph	0	1	2	3	4	5	6	7	8
% in population	2	6	11	20	22	20	11	6	2

The positions of the baits within each metre-square were determined in the usual manner (see Chapter III) and were marked onto a copy of the grid. Playing-cards were then used to ensure that the colours of the baits were randomly distributed within each quarter of the plots of the first and subsequent populations.

A mark on each card indicated the colour it represented. The relative proportions of the marked cards and their total number reflected the constitution and number of baits that were to be distributed. After being thoroughly shuffled the cards were dealt out and the ensuing order of the colours was systematically superimposed on the positions of the baits marked on the copy.

The populations were continuously observed during presentation and were maintained in the normal manner, by frequent replacement of eaten baits.

(iii) Changing the compositions of the populations

All previous experiments involved the presentation of populations with constant proportions of two or three colours. In each of the present studies the compositions of the populations were periodically altered. This was carried out after a certain fixed percentage of baits had been removed by the birds. As a consequence of selection (or random sampling variation) the relative numbers of surviving baits were likely to differ from the original proportions. A new population (or 'generation') of the original size (see below) was then constituted, such that it contained the morphs in the same proportions as had survived predation.

The point at which the composition of a given population should be changed was governed by the following considerations. Ideally, the absolute number taken should be as large as is practicable. This would reduce possible errors due to sampling variation (caused, for example, by differences in the numbers of visits by different birds). Since it was hoped to change the population about once a day, the main limiting factor was the rate of predation. Thus the populations were changed when 100 and 70 baits had been taken from

experiments 1 and 2 respectively. The sizes of the populations were respectively 1,000 and 500. The presentation of so many baits would, of course, be impractical under the standard conditions of two baits per square metre. Instead, the smaller 'presented-populations'¹ were considered as samples of the larger populations. In addition to the 100 baits offered in experiment 3, there were 900 in reserve, whilst in experiment 4, 200 baits were offered with 300 in reserve.

For authenticity, the percentage of baits taken from the population should be of the same order of magnitude as in predation on natural populations. The proportions used, 10% (expt. 3) and 14% (expt.4), are not unreasonable values, in the light of our present knowledge (for general examples, see Lack 1954). Few data are available for predation on polymorphic prey, but Cain and Sheppard (1954a) estimated that thrushes eliminated about 8.6% of 10,000 individuals in about a fortnight.

After the specified number had been taken, the baits were removed from the plot and the new frequencies were estimated. This calculation often resulted in the computation of fractions of baits. For the purposes of estimating the constitutions of the presented-populations, the fractions were rounded-off to the nearest whole number.

(c) Practicability of method

The setting up of the presented-populations was a slow process initially, simply because of the variety of baits involved. After practice the reactions of the human 'predator' improved. It is also interesting to note that at first I was unable to identify

¹In the following pages 'populations' refers to the overall numbers of baits (i.e. 1,000 and 500). The term 'presented-population' is self-explanatory.

Table 50

Experiment 3. Numbers of baits in whole populations ($N = 1000$) after 9 generations of selection. The Table gives for each population χ^2 values for the deviation of its composition from the original distribution, its mean $\bar{x}$ (with 95% confidence limits) and its standard deviation σ .

GENERATION	0	1	2	3
0	20.00	20.94	21.36	21.68
1	60.00	57.30	48.89	47.96
2	110.00	104.73	98.93	89.68
3	200.00	199.56	191.19	179.81
4	220.00	218.26	222.44	220.54
5	200.00	203.97	215.33	228.10
6	110.00	117.90	123.96	129.22
7	60.00	55.20	54.14	57.05
8	20.00	22.04	23.68	25.95
$\chi^2_{(8)}$ (deviation from generation 0)	-	1.67	7.88	17.57
95% confidence limit (upper)	4.107	4.136	4.205	4.274
$\bar{x}$	4.000	4.029	4.099	4.168
95% confidence limit (lower)	3.893	3.922	3.993	4.062
σ	1.733	1.730	1.715	1.719

accurately the colour of a given bait lying in position on the grass, unless it happened to be one of the two extremes - the familiar 0's, and 8's. Identification of the colours was necessary whenever the baits were removed from the grids. On picking up a bait I attempted to assess its colour before transferring it to its corresponding compartment in a tray. It was at this stage that errors of identification became obvious. With time I appeared to become more proficient but never attained 100% accuracy. Unfortunately it was impracticable to keep a record of my responses.

(d) Preliminary study: experiment 3

(i) Materials and methods

The experiment was carried out on a lawn in Portobello, Edinburgh, in September 1969. The size of the lawn limited the presented-population to a 10 m x 10 m grid containing 100 baits. As already mentioned, the size of the whole population was 1,000 and its composition was altered after 100 (=10%) baits had been removed. This figure was adhered to as closely as possible, so as to reduce error.

The first, normally-distributed, population (0) was presented on 18th September. By the end of a week, three further populations (generations) had been presented. Predation was restricted to blackbirds alone and there were at least two males and two females. Individual birds could not be reliably recognised.

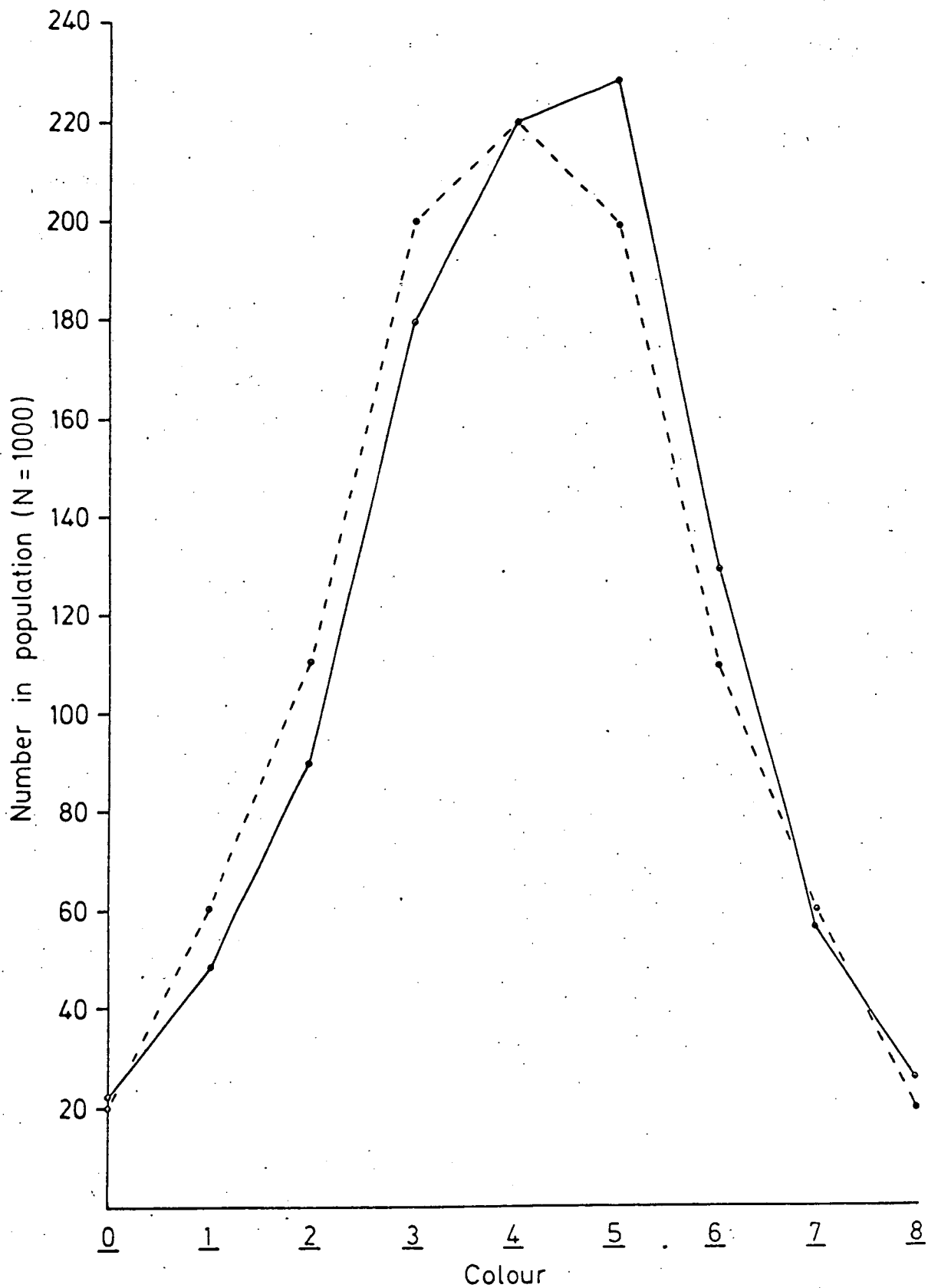
(ii) Results and discussion

Response of population to selection

The compositions of the four generations are given in Table 50. Comparison of each population with the original composition shows

Figure 12

'Normal distribution' experiment 3. Morph-frequencies of population before (broken line) and after (unbroken line) 3 generations of selection.



increased deviations with time. After the third and last generation of selection, this departure was statistically significant (see values of χ^2 given in Table 50).

Figure 12 illustrates graphically the relative frequencies at the beginning (generation 0) and end (generation 3) of the experiment. The shape of the latter graph gives the impression that it is skewed towards the 'greener' half of the distribution. Its modal colour is now 5 and each of the green colours (5, 6, 7, 8) is at a higher frequency than its respective brown counterpart (3, 2, 1, 0).

Assuming that the populations have continuous distributions, we can calculate their means and standard deviations. These are given in Table 50 with the 95% confidence limits for the means. Each successive generation has an increased mean, supporting the view that the populations were becoming 'greener'. Populations 1, 2 and 3 have lower standard deviations than that of 0, implying less variation about the means.

Earlier experiments (see Chapters V, VI, VII, VIII) revealed that blackbirds and thrushes generally prefer 0's to 8's when presented in 'spaced-out' populations. The present results are undoubtedly partly due to a tendency for the birds to take the browner colour. However, the situation is complicated by at least two other factors.

First, there is some evidence for frequency-dependent selection. That is, both of the rarest colours, 0's and 8's, apparently enjoyed relative protection from predation and consequently increased in abundance. In the absence of frequency-dependent selection and in the presence of preferences for brown, we might expect the 0's to

Table 51

Pooled data for predation by female and male blackbirds on populations (0,1,2) of experiment 3. Two pairs of birds were probably involved.

Females

Colour	Numbers taken	% of total
0	3	1.7
1	27	15.7
2	35	20.3
3	52	30.2
4	38	22.1
5	10	5.8
6	5	2.9
7	2	1.2
8	0	0.0
	172	99.9

Males

Colour	Numbers taken	% of total
0	2	1.7
1	1	0.8
2	12	10.1
3	24	20.2
4	26	21.8
5	25	21.0
6	11	9.2
7	17	14.3
8	1	0.8
	119	99.9

have decreased in frequency, as did the 1's, 2's and 3's.

Now due to the close visible similarity between the 8's and 7's, we might predict that the latter also would have proliferated within the population, particularly as the other two types of green (6's and 5's) exhibited such a trend. In fact the 7's suffered a slight negative change. This brings us to the second factor complicating the results given in Figure 12: the behaviour of the predators. The result for the 7's is probably associated with the heterogeneity of the birds' responses, as we shall see.

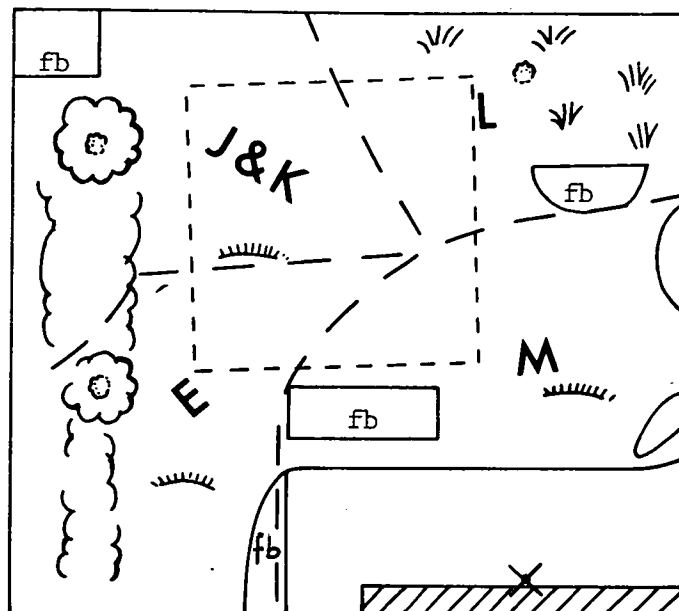
Behaviour of the birds

The three presented-populations (0, 1 and 2), being one-tenth of the size of the overall populations, did not differ significantly in composition. It is therefore legitimate to pool the results of predation on these populations. Accurate data for individual predators cannot be obtained however, since the blackbirds were unmarked. But the birds could be classified according to sex and a comparison of the results for males and females gives an indication of differences in behaviour.

Table 51 gives the pooled results for predation by the two sexes and these data are also presented as percentages. The distributions of the two sets of data differ significantly ($P < 0.001$, Kolmogorov-Smirnov test). Predation by the females is heavily biased towards the browner morphs. Each of the green types (5, 6, 7, 8) was taken at a lower frequency than its brown counterpart (3, 2, 1, 0). Amalgamation of the

Figure 13

Site of plot in 'normal distribution' experiment 4 (March-April 1970), showing boundaries of blackbird territories. Compare with Figures 10a and 10b, page 147.



KEY

----- outline of plot.

—bush

○—tree

fb—flower bed

—lawn

—long grass

—territorial boundary

—observation point

Scale
0 5 10 Metres

four types in each category shows that 71 greens were removed as opposed to 156 browns. If a similar calculation is carried out for the males, we find that 54 greens and 39 browns were taken; in other words, greens were preferred. Inspection of the data reveals that an excessive predation of 7's probably contributes to this result. Field observations seemed to indicate that a single bird was concentrating on searching for 7's.

(a) Experiment 4

The pilot experiment demonstrated the feasibility of working with nine types of similarly coloured baits and paved the way for a more prolonged study with individually recognisable birds.

(1) Materials and methods

This second experiment took place at my Reading home during March - April 1970. The reader is referred to p.148 for details of the environment. Though of similar concept, this study differed from the previous one in the following points:

A. Prior to the presentation of generation 0, the birds were familiarized with 4's for one week. It was hoped that this procedure would nullify the birds' overall bias towards browns. All the participants of the later part of the experiment were observed feeding on the training diet.

B. An attempt was made to quicken the response by lowering the population from 1,000 to 500 whilst raising the selection to 20%. In fact a value of 14% was ultimately used because the rate of predation was slow.

Table 3. Numbers of bars in whole population ($N = 900$) after 10 generations of selection. The table gives for each generation, Experiment 4, χ^2 values for its goodness-of-fit to the original distribution, its mean $\bar{x}$ (with 95% confidence limits) and its standard deviation σ .

GENERATION		0	1	2	3	4	5	6	7	8	9	10
COLOUR	0	10.00	11.76	13.10	12.73	13.74	13.53	15.12	13.05	15.21	15.77	16.21
	1	30.00	35.28	38.18	35.76	38.61	36.42	40.24	41.35	38.86	36.84	33.91
	2	55.00	56.47	56.20	54.13	54.13	58.92	64.94	69.16	73.60	68.74	69.11
	3	100.00	100.00	98.02	95.21	98.47	92.74	91.18	89.41	87.90	84.61	81.91
	4	110.00	102.35	89.50	82.00	73.41	77.69	73.07	66.97	68.73	67.70	60.81
	5	100.00	91.76	96.63	102.80	102.30	102.00	95.10	97.52	97.34	102.80	104.51
	6	55.00	55.29	57.14	59.81	61.34	59.16	53.16	55.34	54.01	52.53	55.91
	7	30.00	35.28	38.18	43.78	45.10	45.06	51.84	49.18	43.24	46.83	50.41
	8	10.00	11.76	13.10	13.88	12.82	14.78	15.38	18.05	21.04	27.91	26.91
$\chi^2_{(8)}$ (deviation from generation 0)		-	3.73	10.47	17.56	25.26	23.11	40.18	45.53	46.69	55.94	76.11
95% confidence limit (upper)		4.107	4.138	4.165	4.260	4.235	4.250	4.206	4.221	4.188	4.273	4.311
$\bar{x}$		4.000	3.979	4.001	4.095	4.068	4.081	4.032	4.047	4.013	4.097	4.111
95% confidence limit (lower)		3.893	3.820	3.837	3.930	3.901	3.912	3.858	3.873	3.838	3.921	3.911
σ		1.733	1.818	1.875	1.894	1.920	1.925	1.989	2.000	2.009	2.030	2.011
GENERATION (cont.)		11	12	13	14	15	16	17	18	19	20	
COLOUR	0	18.63	19.85	19.23	19.41	21.20	23.03	21.03	23.24	20.14	19.88	
	1	36.73	41.45	41.61	44.99	49.53	47.30	43.46	36.51	33.31	29.36	
	2	66.83	65.43	74.69	72.59	72.11	73.03	75.77	80.95	84.05	77.78	
	3	86.16	82.54	82.79	89.45	84.63	85.02	80.41	61.97	52.53	49.34	
	4	57.31	55.27	52.82	42.85	47.07	47.90	46.49	48.14	56.23	58.21	
	5	99.45	98.40	92.92	81.28	74.01	63.80	60.36	67.72	61.59	61.01	
	6	52.83	48.73	43.09	44.37	38.44	38.06	37.36	36.39	33.16	37.31	
	7	53.35	56.52	57.55	17.67	72.21	76.56	84.55	87.66	96.56	102.80	
	8	28.71	31.88	35.26	37.41	40.80	45.33	50.49	57.42	62.40	64.27	
$\chi^2_{(8)}$ (deviation from generation 0)		91.93	118.39	144.93	192.07	234.94	285.62	351.06	432.84	520.48	561.33	
95% confidence limit (upper)		4.336	4.341	4.311	4.349	4.339	4.378	4.499	4.626	4.744	4.867	
$\bar{x}$		4.151	4.152	4.118	4.151	4.136	4.171	4.289	4.414	4.532	4.657	
95% confidence limit (lower)		3.966	3.962	3.925	3.953	3.933	3.964	4.079	4.202	4.320	4.447	
σ		2.110	2.163	2.195	2.261	2.317	2.363	2.389	2.420	2.424	2.406	

C. The size of the presented-population was 200.

D. Seven *Turdidae* were involved. All the five blackbirds were colour-ringed or otherwise recognisable. Two unringed songthrushes also participated in the experiment but it was impossible to distinguish between them. With the exception of the male blackbird E¹, none of the birds had been involved in previous experiments at the site. Frequent territorial displays occurred throughout the experiment and revealed the approximate arrangement of the territorial boundaries shown in Figure 13. Robins also fed on the baits occasionally but since the numbers taken were small, this species was disregarded for the purposes of the experiment.

Population O was presented on 21st March in a 10 m x 10 m grid sited as shown in Figure 13. By 15th April 20 generations of selection had been completed.

(ii) Results and discussion

Response of population to selection

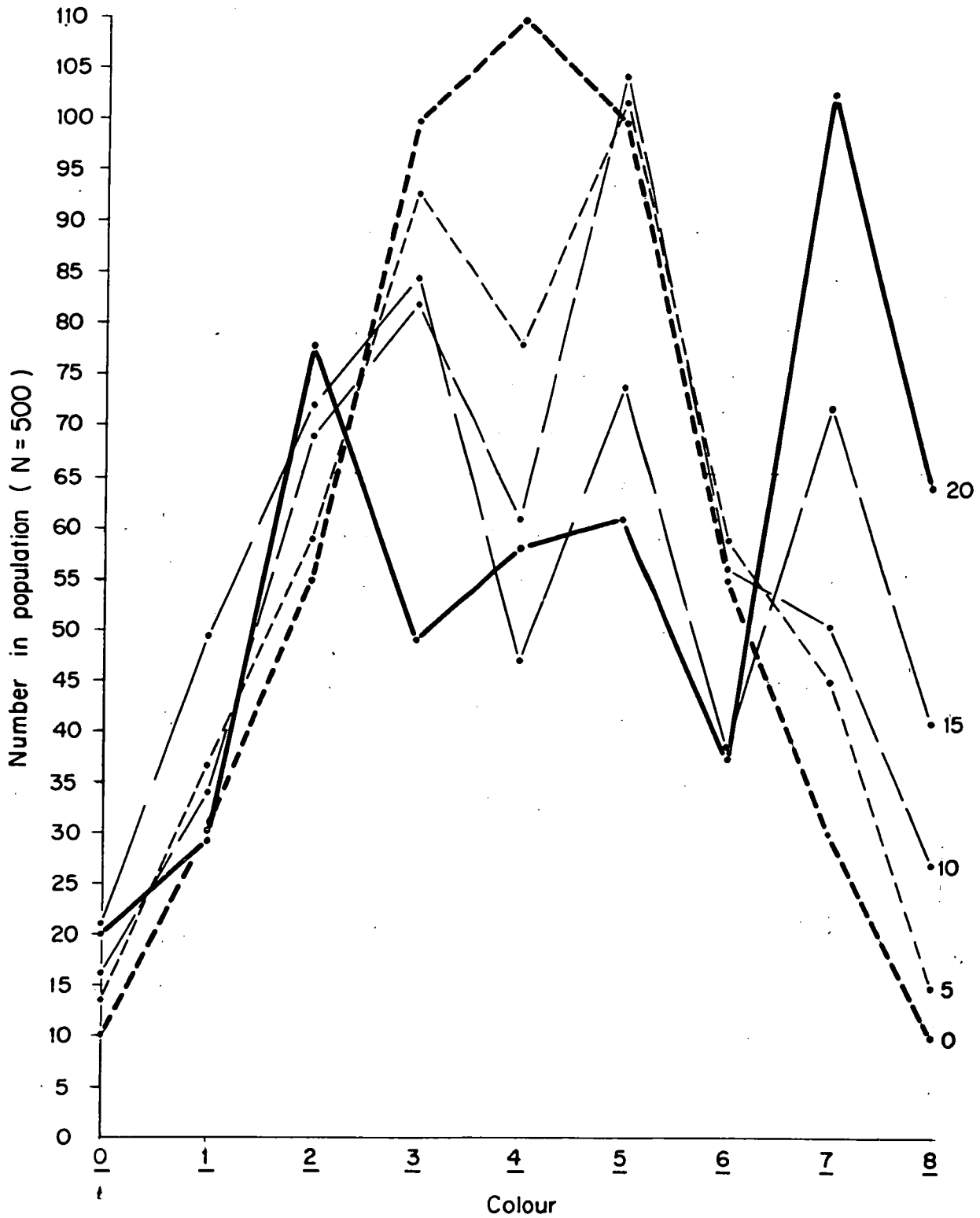
The complete data for the compositions of the populations are given in Table 52, p.222. As indicated by the values of χ^2 , the distribution rapidly became significantly different from the original frequencies (bearing in mind that $P = 0.05$ when $\chi^2 = 26.13$, for 8 degrees of freedom). The Table also gives the means and standard deviations of the populations. These data show that the distributions were gradually becoming greener, but with more and more variation about the means.

We must examine these changes in more detail. The evolution of the populations can best be visualised from a graphical presentation

¹For the previous history of E, see Chapter VIII.

Figure 14

'Normal distribution' experiment 4. Morph frequencies in populations for every fifth generation (0, 5, 10, 15, 20).



of the data in Table 52. This is done in Fig. 14. In order to avoid confusion in discerning the main trends, every fifth generation is shown. Certain features are immediately obvious. The first relates to the increase in variance noted above: the centres of the distribution become progressively 'eaten-away' during the course of the experiment. For the first twelve visits or so, the range of this depression is confined mainly to the 4's; in contrast, the two most similar colours, 3's and 5's suffer appreciably less change. Apparently, then, the birds were tending to concentrate on eating 4's. On the basis of previous 'training' experiments (particularly those described in the first part of this Chapter) we can presume that this effect was a result of the birds' previous experiences with this colour. By the end of the experiment, 3's and 5's were apparently also being taken in relatively greater numbers, for their frequencies decreased within the population.

Correspondingly, the 7's and 8's underwent two- and five-fold increases in numbers. As in the previous experiment, such effects could be caused by an overall aversion for the greener colours. If this were the case then we would expect similar results for the 6's (a colour that I myself often confused with 7's). In fact, the 6's actually decreased in numbers. We will presently see that this effect was probably the result of the idiosyncrasies of a single male blackbird.

Behaviour of the birds

The birds each took too few baits for meaningful conclusions to be derived for predation on single populations. However, there

are no significant differences in the proportions within every three (or two¹) generations and the results for individual² predation over these periods can consequently be amalgamated. Table 54 (pages 256 and 257) gives these data in full and Figures 15 to 21 (pages 229 to 243) present them graphically.

In the Figures the predation on a given colour is expressed as a percentage of the total number of baits eaten by the relevant bird (or birds, in the case of the thrushes). Specific types of lines are used for each of the predators and the average compositions of the populations over every three generations are shown by the boldest lines. Predation by the female blackbird M is omitted from the first two Figures since totals of only five baits and one bait were taken.

Fig. 15 for predation over the first three generations (0 - 2), shows that all the depicted birds tended to take more 4's than expected. In other words, all the five points are above the mean percentages of 4's offered. Furthermore, male blackbirds J and L took relatively more 4's than any other colour whilst the thrushes appear to have been concentrating on both 4's and 5's. The most striking result is that of J which took more than twice as many 4's as its next most favoured colour, 5. The male blackbird E and the female K took relatively more 3's than 4's.

Over generations 3 to 5 (Fig.16) the birds still tended to take more 4's than expected, though again this was not necessarily the preferred colour (K took relatively more 3's, for example).

¹Since 20 populations were presented they can be divided into six groups of three and one of two (generations 18 + 19).

²Predation by the individual songthrushes could not be recorded because the birds were indistinguishable. By necessity the data for the thrushes refer to their combined efforts, and in the following pages the two birds are treated as one; this is simply for ease of presentation.

Table 53

Mean colours of baits taken by each bird over every three (or two) generations in Experiment 2, with standard errors. Calculated from data given in Table 54. The average means and standard errors of the presented-populations are also given.

GENERATIONS	B I R D S							Presented-population
	E	J	K	L	M	T'o		
0 - 2	3.711 $\pm$ 0.376	4.053 $\pm$ 0.266	3.407 $\pm$ 0.482	3.710 $\pm$ 0.590	-	3.833 $\pm$ 0.468	3.993 $\pm$ 0.255	
3 - 5	4.075 $\pm$ 0.610	4.774 $\pm$ 0.310	4.037 $\pm$ 0.528	4.000 $\pm$ 0.622	-	4.135 $\pm$ 0.540	4.091 $\pm$ 0.267	
6 - 8	3.598 $\pm$ 0.500	5.321 $\pm$ 0.374	3.862 $\pm$ 0.636	3.741 $\pm$ 0.759	2.929 $\pm$ 0.808	3.269 $\pm$ 0.472	4.020 $\pm$ 0.280	
9 - 11	2.993 $\pm$ 0.523	5.275 $\pm$ 0.260	3.600 $\pm$ 0.661	3.778 $\pm$ 0.664	3.737 $\pm$ 1.306	3.969 $\pm$ 0.436	4.142 $\pm$ 0.290	
12 - 14	3.783 $\pm$ 0.728	5.192 $\pm$ 0.365	3.476 $\pm$ 0.698	4.484 $\pm$ 0.635	3.727 $\pm$ 0.567	3.705 $\pm$ 0.575	4.140 $\pm$ 0.303	
15 - 17	3.556 $\pm$ 0.852	4.700 $\pm$ 0.507	3.208 $\pm$ 0.809	3.258 $\pm$ 0.797	3.031 $\pm$ 0.649	4.578 $\pm$ 0.541	4.051 $\pm$ 0.340	
18 - 19	3.700 $\pm$ 1.122	5.036 $\pm$ 0.702	3.294 $\pm$ 0.719	3.500 $\pm$ 1.040	2.583 $\pm$ 0.885	2.870 $\pm$ 0.811	4.328 $\pm$ 0.351	

In contrast to the other eight colours, 4's were underpredated by only one bird. Surprisingly, perhaps, in the light of the preceding three generations, this predator was blackbird J. As can be seen from Figure 16, J was now concentrating on searching for 5's and these baits were taken over three times more frequently than any other. The differences between the proportions taken over generations 0 - 2 and 3 - 5 are statistically significant ($P < 0.001$, Kolmogorov-Smirnov test on data shown in Table 54). In other words there appears to have been a distinct change in preference by this bird.

The five remaining Figures show that J was persistent in its treatment of 5's. These were always the most preferred baits, though 6's (Figs. 17, 18 and 19) and 7's (Fig. 17) were sometimes also taken at relatively high frequencies. It is obvious from the graphs that this bird preferred the greener baits to the browner ones and this point is well made by Table 53 which shows the mean colours taken by each of the birds.

With regard to the remaining birds, the most consistent trend from generations 6 - 9 (Figure 17) onwards, is a tendency for the graphs to be skewed in the direction predicted on the basis of preferences for brown. This is especially noticeable in Figs. 17 and 18, whilst reference to Table 53 shows that in contrast to the means of the average presented-populations, the birds tended to take samples with means below 4.

5. DISCUSSION

(a) Stimulus generalisation and the specificity of conditioning

The training experiments demonstrated that wild birds can

(cont. p.244)

Pages 230 to 243: Figures 15 - 21

Percentages of the eight types of baits taken
by each bird in 'normal distribution' experiment 4
over every 3 generations. The percentage average
compositions of the populations are also shown.

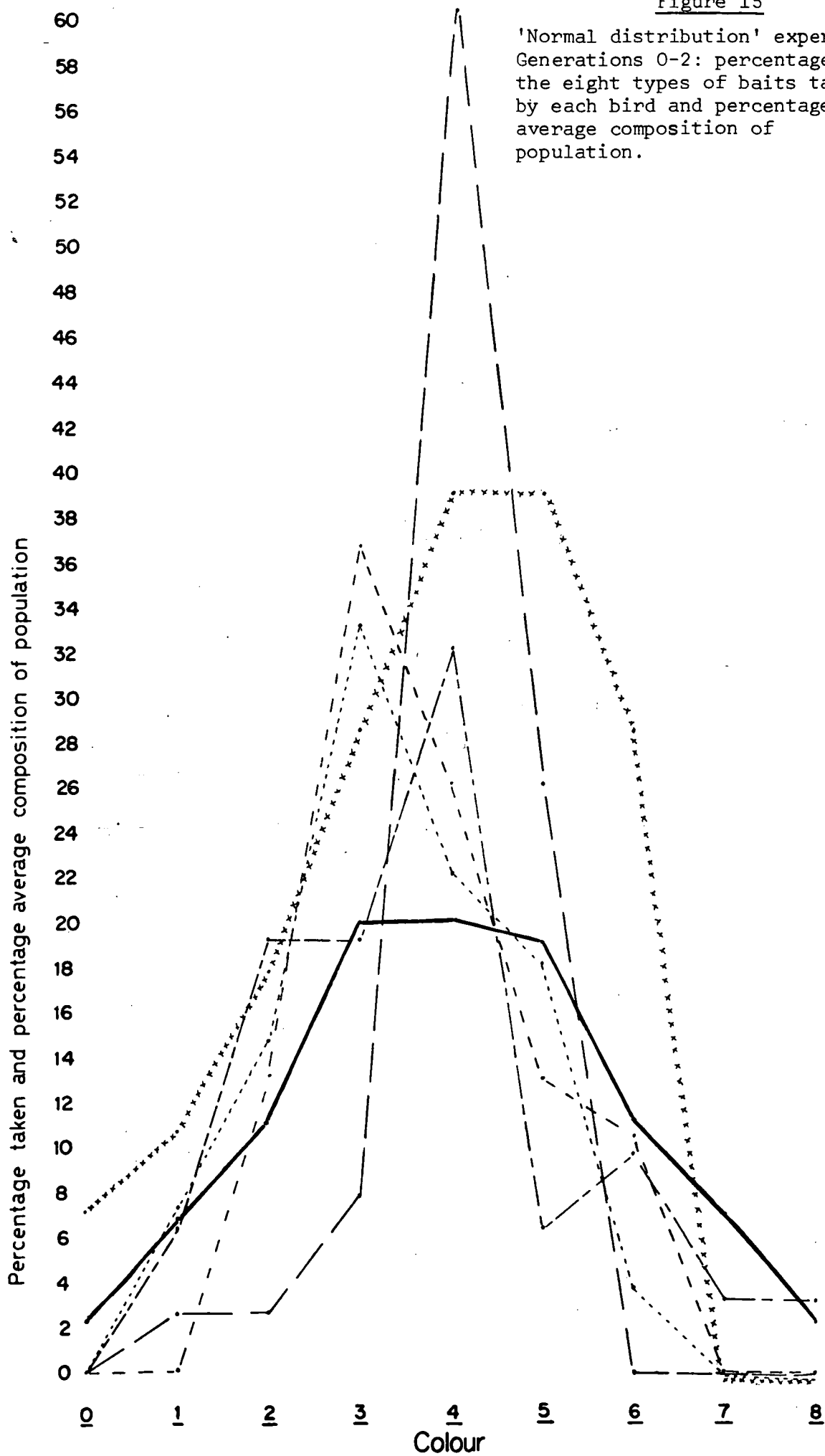
611 1958

Key to Fig. 15

-----	predation by blackbird E
_____	" " " J
-----	" " " K
-----	" " " L
x x x x x x	" " songthrushes
—————	average composition of population

Figure 15

'Normal distribution' experiment 4.
Generations 0-2: percentages of
the eight types of baits taken
by each bird and percentage
average composition of
population.

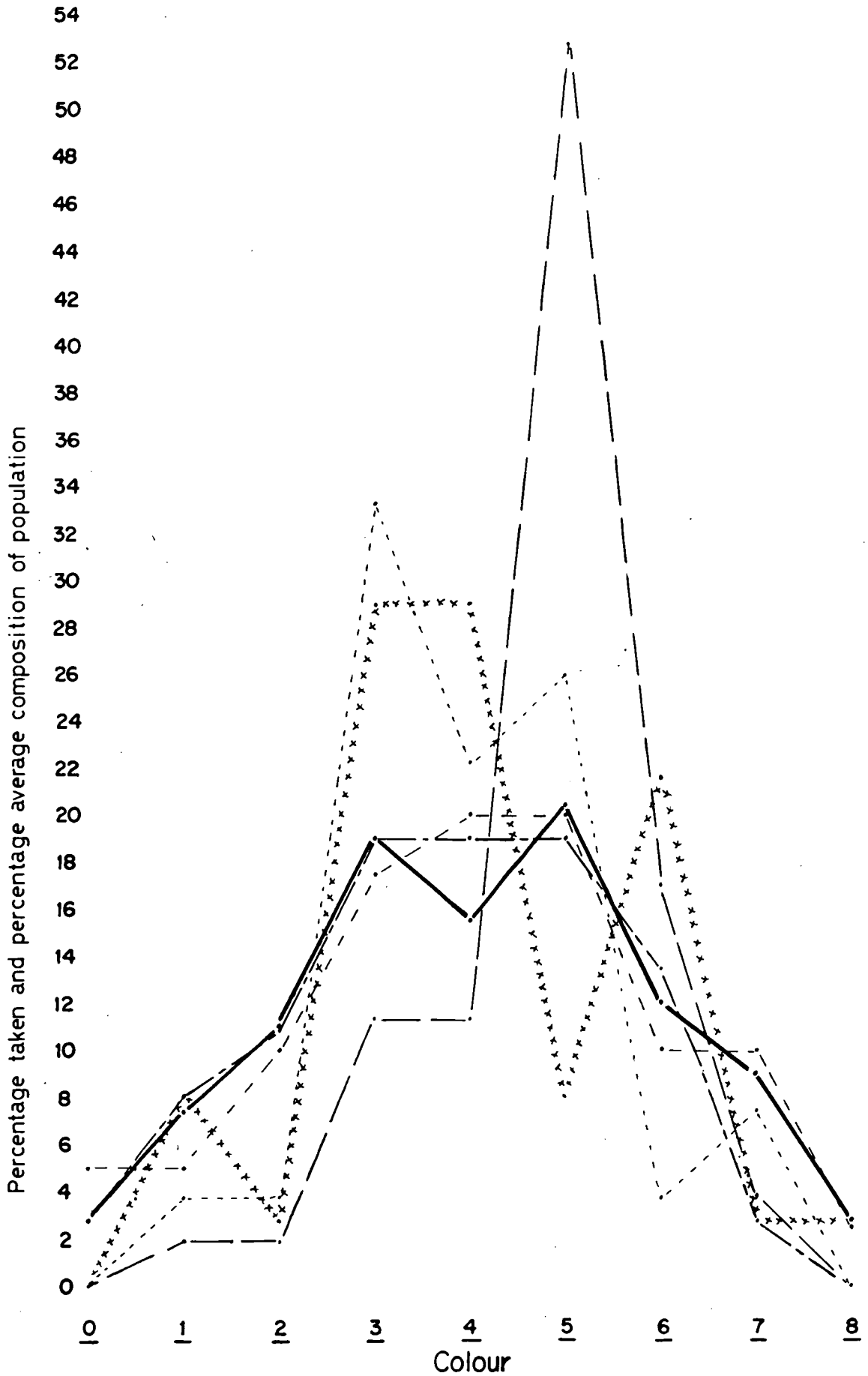


Key to Fig.16

_____	predation by blackbird E
_____	" " " J
_____	" " " K
_____	" " " L
x x x x x x x	" " songthrushes
_____	average composition of population

Figure 16

'Normal distribution' experiment 4. Generations 3-5:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.

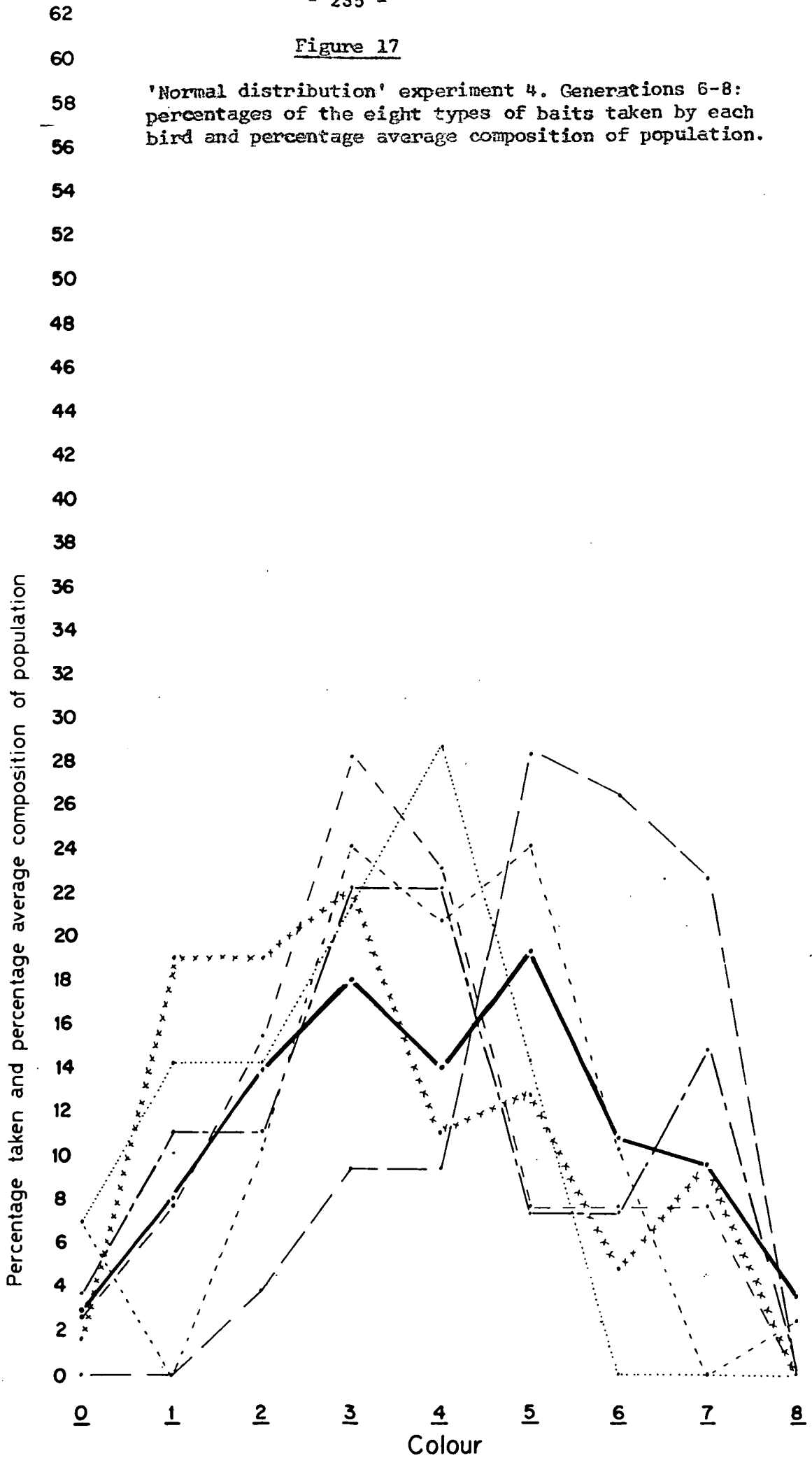


Key to Fig. 17

-----	predation by blackbird E
_____	" " " J
-----	" " " K
_____	" " " L
.....	" " " M
xxxxxxx	" " songthrushes
_____	average composition of population

Figure 17

'Normal distribution' experiment 4. Generations 6-8:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.

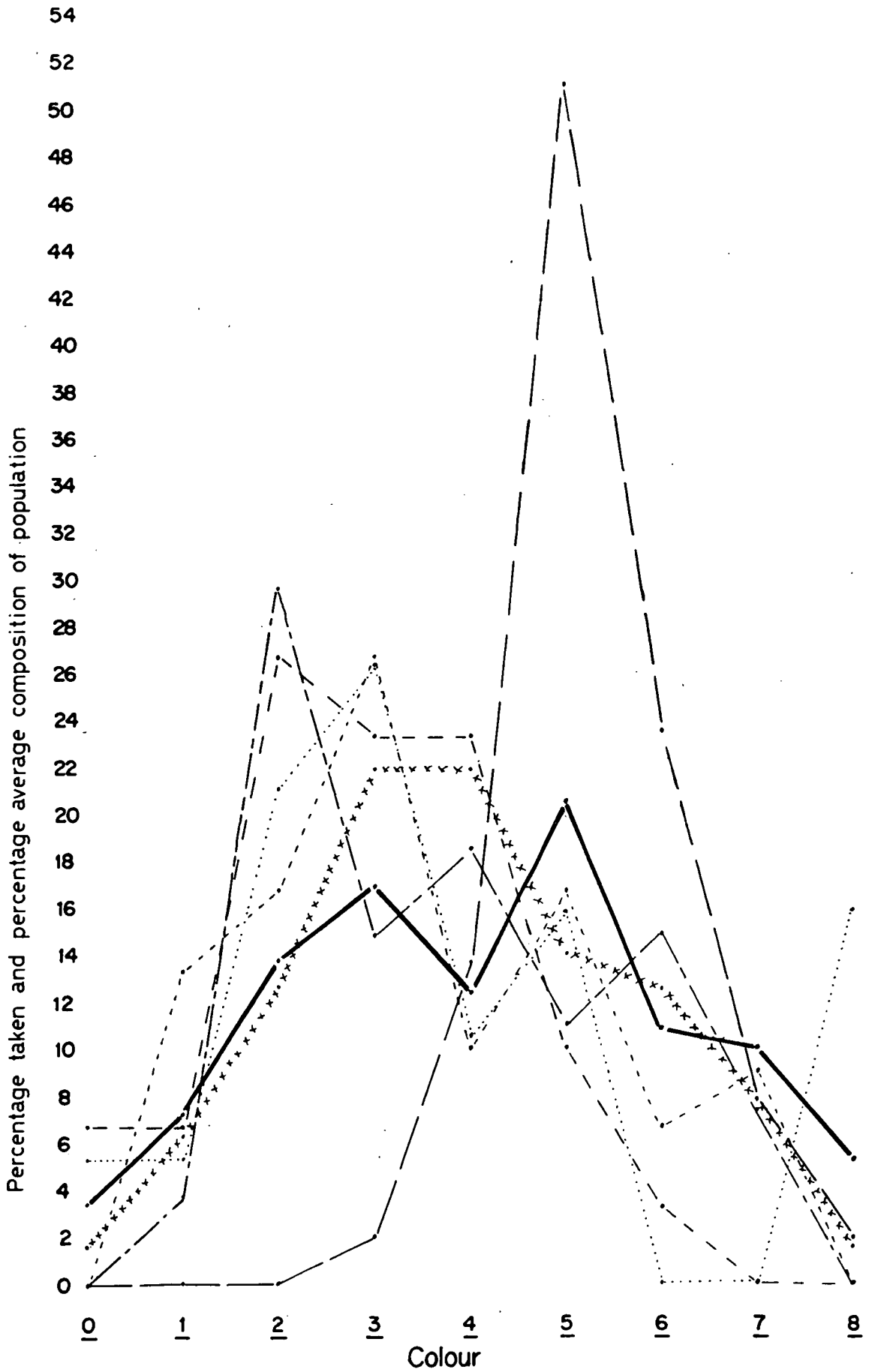


Key to Fig. 18

-----	predation by blackbird E			
_____	"	"	"	J
- - - - -	"	"	"	K
_____	"	"	"	L
.....	"	"	"	M
x x x x x x x	"	"	songthrushes	
_____	average composition of population			

Figure 18

'Normal distribution' experiment 4. Generations 9-11:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.

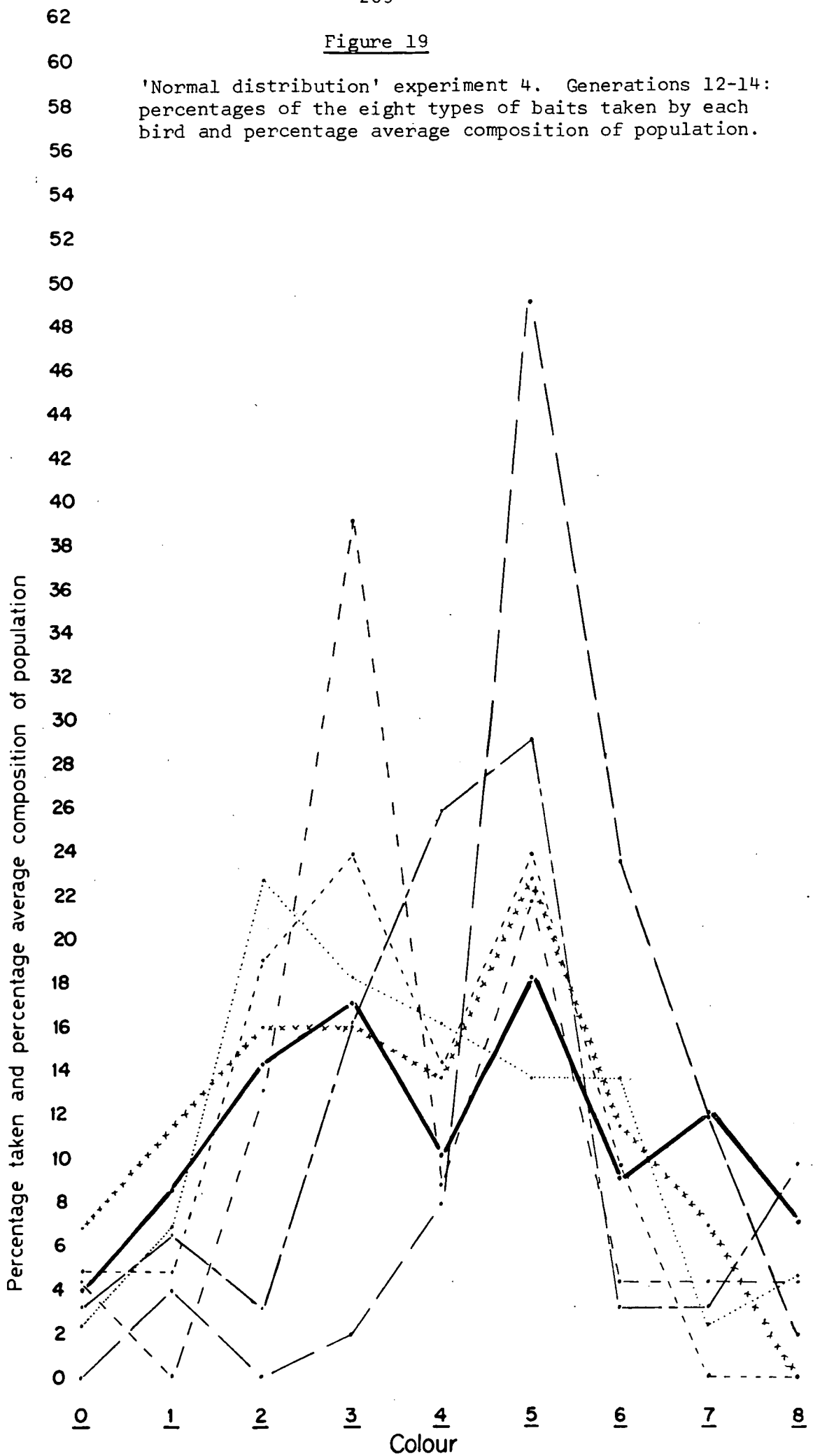


Key to Fig. 19

-----	predation by blackbird E
____ _	" " " J
-----	" " " K
____ _	" " " L
-----	" " " M
x x x x x x	" " songthrushes
_____	average composition of population

Figure 19

'Normal distribution' experiment 4. Generations 12-14:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.



Key to Fig. 20

— — — — —	predation by blackbird E
— — — — —	" " " J
- - - - -	" " " K
— - — — —	" " " L
- - - - -	" " " M
x x x x x x	" " songthrushes
—————	average composition of population

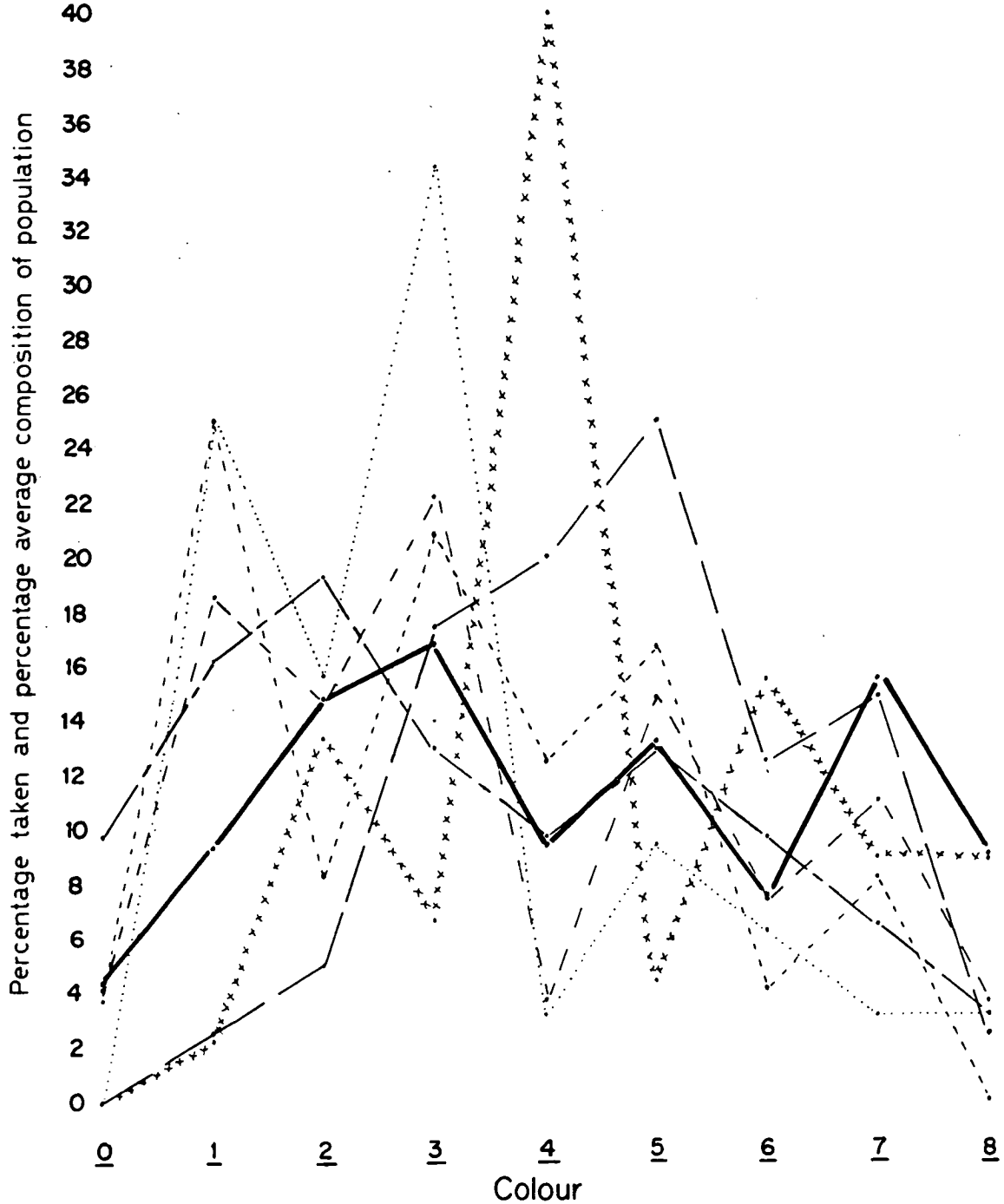
Figure 20

'Normal distribution' experiment 4. Generations 15-17:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.

Percentage taken and percentage average composition of population

62
60
58
56
54
52
50
48
46
44
42
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0

0 1 2 3 4 5 6 7 8
Colour

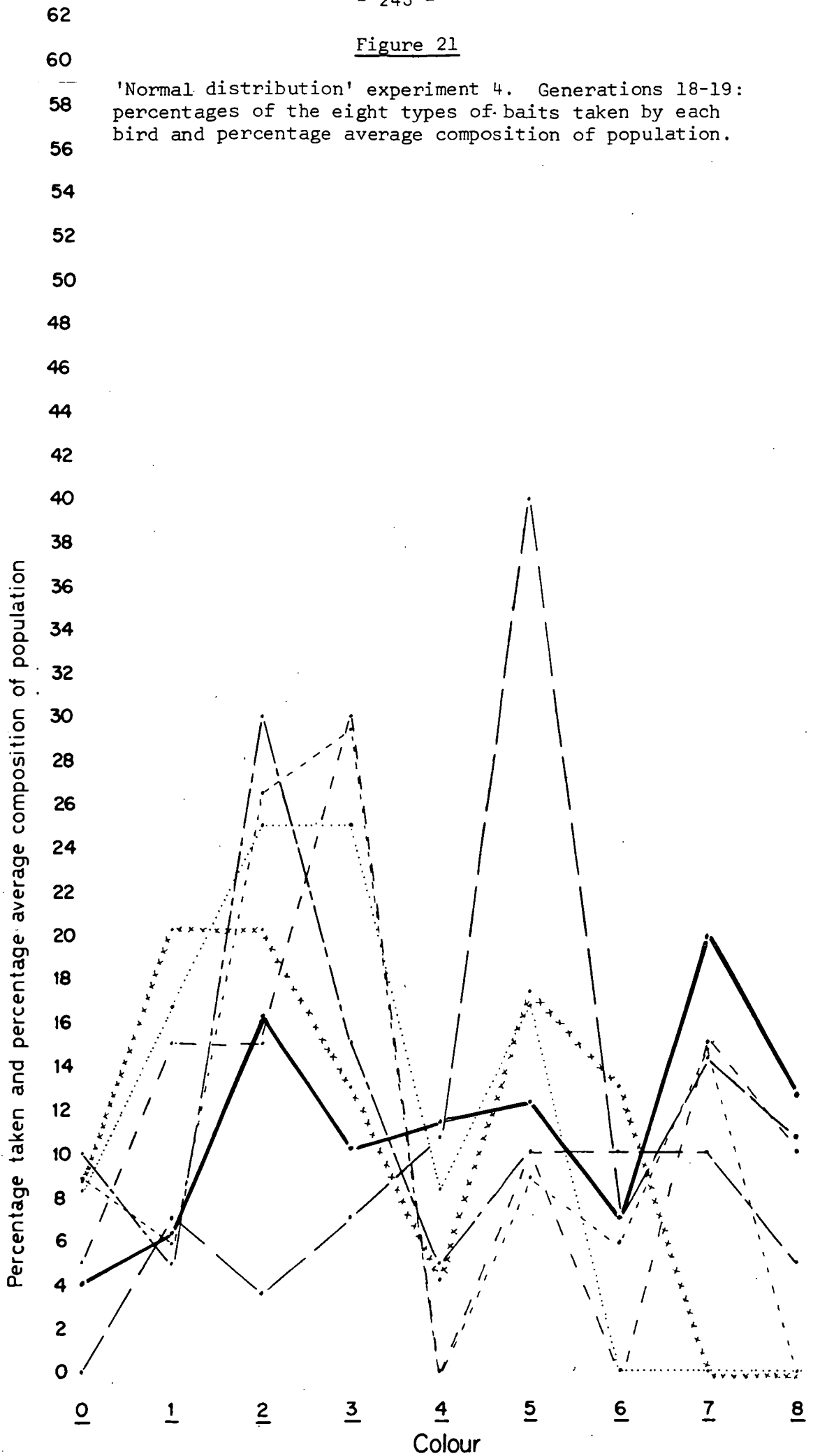


Key to Fig. 21

-----	predation by blackbird E			
_____	"	"	"	J
-----	"	"	"	K
____-____-	"	"	"	L
-	"	"	"	M
x x x x x x	"	"	songthrushes	
_____	average composition of population			

Figure 21

'Normal distribution' experiment 4. Generations 18-19:
percentages of the eight types of baits taken by each
bird and percentage average composition of population.



discriminate between two prey of similar colour. Similar results were obtained for some of the birds in experiment 4, though in this case the morphs were even less alike. We must now examine these findings in greater detail and put them into perspective with our present knowledge of the behaviour of predators.

On learning to distinguish between a number of given stimuli, animals tend to generalise their subsequent responses to include similar cues. Thus in the classical experiments of Pavlov (1927) dogs were trained to salivate in response to a stimulus that preceded a reward of food. In other trials, the dogs were presented with stimuli not followed by food. Pavlov found that not only did the positive stimulus elicit salivation, but other similar stimuli did also. And the converse held true for the negative stimulus and ones similar to it.

After further training, animals can be induced to relax their generalisation and they may eventually become capable of differentiating between similar stimuli. An early example of such discrimination is quoted by Pavlov (op.cit.). Gubergritz, a student of his, was able to train dogs to distinguish between light grey and dark grey stimuli. More recently, Skinner (1965) for example, has shown that pigeons can learn to discriminate between triangles of particular sizes, whilst Sutherland (1969) has demonstrated that various subjects (rats, goldfish, octopuses) can differentiate between similar shapes or patterns. Different methods of training can be used in such 'discrimination-learning' experiments (for summary, see Switalaki et al. 1966), but most, at some stage, involve the presentation of a stimulus associated with a negative reward.

It is of obvious advantage for a predator to learn to distinguish between, say, a distasteful and palatable prey. Hence inexperienced birds will take a wasp as readily as a fly, but soon learn to recognise the distinctive warning-colour pattern of the latter (Mostler 1935). On the other hand, predators should also benefit in being able to generalise on such negative stimuli. The evolution of Batesian mimicry is commonly regarded as arising through the agency of a combination of these two types of behaviour. Various workers (e.g. Mühlmann 1934, Sexton 1959, Morrell and Turner 1970, Duncan and Sheppard 1959) have investigated the degree to which a mimic must resemble a model before being mistaken for it.

But what implications have the above studies to the present work? They show that predators, including birds, are certainly capable of a high degree of specificity in their response to conditioned stimuli. Yet it must be re-stressed that my experiments deal with types of equally-palatable prey. These differ only with regard to stimulus (i.e. colour), not reward. The apparently negative attributes of the unfamiliar types can only be associated with their novelty. We must now consider, in conjunction with the present results, the evidence for discrimination learning and stimulus generalisation by predators searching for similar palatable prey.

One example illustrating the specificity of searching images for palatable prey has been mentioned in Chapter II. Do Ruiter (1952) showed that caged birds are capable of distinguishing between stick-caterpillars and the twigs of their host plant. The birds were not totally adept at recognising the caterpillars, however, for

some of the twigs were apparently mistaken for prey and were consequently pecked. When other species of twig were presented some of the birds pecked only those sticks that most resembled the larvae in size, shape and colour.

For the most relevant data pertaining to discrimination on the basis of differences in colour alone we must again turn to the work of Croze (1967, 1970). In his own words (page 43, 1970), the question he was asking was: "how similar in terms of colour, form and structure does a subsequent prey have to be in order to elicit the response associated with the sample?" Here we are mainly concerned with the first type of visual cue.

Croze first trained a pair of wild crows to search for mussel shells covering pieces of meat. These prey were made by coating the shells with a layer of sand prior to being painted red. The experiment was carried out on a background of shingle.

After nearly two months, unrewarded test populations were occasionally presented. These consisted of 48 prey arranged in pairs. A standard red mussel and a new shell comprised each pair and the two shells were separated by two metres. The new shells were distinguishable from the standard mussels by one of the three criteria mentioned above, namely: colour, form or surface texture. All the prey-types were meant to be camouflaged against the shingle. Colour variants were made from similarly shaped mussel shells as were used for the standard reds but were painted either a redder, yellower or bluer shade of red, or yellow or black. It is the results of tests involving these forms that are most pertinent to the present discussion.

The main findings were as follows. Though red-red shells were

turned as often as the standard reds the latter were taken first more often from a pair, indicating that the birds were distinguishing between the two. Red-yellows on the other hand were apparently indistinguishable from the standards. Blues were very different in appearance but also appeared more conspicuous; they were taken in smaller numbers. The yellow and blacks were totally overlooked because they were more camouflaged than blues and were equally different from reds. In other words the crows' searching images were highly specific. They tended to predate only those colours that were spectrally the most similar to the standard stimulus.

Despite the obvious differences in experimental design, my findings are comparable with those of Croze. That is to say, the closer the resemblance of an unfamiliar prey to the familiar type, the more likely is it to be taken. For example, the unfamiliar colours in the present training experiments were relatively less protected from predation than the unfamiliar colours of the green-brown experiments described in Chapter V. This will become obvious on comparing, for instance, the predation on the first day after each training session in the two groups of experiments (see Tables 12, 13 and Tables 48a, b).

Although the four khaki-training experiments should strictly not be directly compared, it may be relevant that the two most significant results were those for the first series (see χ^2 values, lowest row, Table 47). We may therefore infer that the birds were more liable to mistake 6's and 2's for 4's than they were 8's and 9's. The results of experiment 4 showed that the seven predators, as a group, took relatively too many of the

familiar 4's from the populations presented at the start. In contrast to the ensuing decrease in the numbers of 4's in the population, the proportions of 3's and 5's remained relatively static. The predators en masse were apparently discriminating between 4's and the two most similar colours. In fact when the data for individual birds were examined we found distinct differences in behaviour.

While all took an excess of 4's, only one bird definitely tended to respond specifically to this colour. In most of the birds extrinsic brown preferences appeared to be interacting with the effects of training. Blackbird J, however, initially discriminated between 4's and 3's, and 4's and 5's. Hence the steep gradient, about a mean value of 4, of the curve shown in Figure 15. This bird later tended to concentrate on searching for 5's and in general he appeared to prefer the greener baits. Assuming that such a preference is representative of his normal behaviour we may conclude that during the start of the experiment it had been modified by the preceding period of training. In contrast to those for the other birds, the graphs for J generally exhibit tall, sharp peaks around the modal frequency of 4's or 5's. In other words, his preferences, whatever their causes, were very specific.

In all the experiments the birds became less specific in their choice as the experiments progressed. As they encountered new types of baits (by chance? cf. Tinbergen 1960) they presumably learned that these too represented food.

Had the training periods in my experiments been longer, the birds' tendencies to select the familiar colour may have been

correspondingly more persistent. In Croze's (1967, 1970) experiments a 'new pair' of crows arrived during the presentation of the conditioned stimulus. These birds had experience of the standard reds for only about one week, whilst the 'older' pair fed on the sample for nearly two months. During the presentation of the test populations, the 'old' pair responded more specifically to the standard red mussel than did the 'new' pair.

(b) Disruptive selection

Experiment 4 has again shown that a group of blackbirds and songthrushes can differ markedly in their individual responses. Another result was that most of the birds, with one notable exception, preferred the browner baits once the effect of the conditioning to 4's had worn off. These two findings agree with the results from other experiments described in this thesis and have been discussed in Chapter VIII.

The effect of the combined predation was to produce a prey population with a greater variance and two modes, with the larger peak in the green half of the distribution. The selection therefore showed signs of being 'disruptive'¹ (Mather 1953) in the sense that the population had acquired two 'optima' through selection against intermediate types. At least three factors contributed to give the selection its overall disruptive effect and these are given below.

¹Dobzhansky (e.g. 1970) prefers the term 'diversifying'.

A. The previous training on 4's resulted in the birds acquiring a preference for these baits, and other morphs were therefore at an advantage. Consequently selection at the beginning of the experiment was disruptive and apostatic. Moreover each bird was behaving in a similar manner to its fellows.

B. As the effects of the training diminished, most of the birds tended to search for the browner baits which resulted in the population becoming skewed towards the greener end of the spectrum. The birds were now more variable in behaviour.

C. One bird (J) preferred 5's and 6's and was largely responsible for the obvious difference between the final relatively low frequencies of these colours in comparison with the high proportions of 7's and 8's. In view of the diverse behaviour of the individual birds it is unlikely that the results shown in Figure 14 could be duplicated in a repeat experiment using 'new' birds.

Mather (1955) has shown that disruptive selection can, under certain conditions, give rise to polymorphism. This contention has been supported by mathematical examination of some special cases (see, for example; Levene 1953, Levine and MacArthur 1966), and by experimental studies on Drosophila, in particular by Thoday and his colleagues (e.g. Thoday and Bean 1959, Gibson and Thoday 1962, 1963). Experiment 4 also seems to support Mather's argument.

There are two (often confused) major aspects of disruptive selection. First, by discriminating against intermediate phenotypes, it may promote polymorphism and maintain the distinctness of the morphs. Second, under certain circumstances, it may be capable of maintaining the polymorphism.

(1) Maintenance of distinctness of morphs

We know of one situation - in mimetic colour-polymorphism - where disruptive selection by predators keeps the morphs visually distinct. This has best been demonstrated by studies on the tropical swallowtail butterflies Papilio dardanus Brown and P. memnon L. (Clarke and Shoppard 1960, 1962; Shoppard 1958, 1969; see also Ford 1964 for review). The females of these palatable species are often polymorphic and each morph mimics a particular distasteful butterfly. There is thus a premium on the close resemblance of the morphs to their appropriate models, and intermediate forms tend to be eliminated by sight-dependent predators.

The results of experiment 4 suggest that disruptive selection by predators may also be capable of promoting and maintaining the visual distinctness of non-mimetic morphs, bearing in mind that the combined effect of the three components of the selection may have given a somewhat unrealistic result (see above, p. 250). The most relevant point is that once the birds had become accustomed to searching for 4's, they were inclined to continue to do so when presented with 'normally-distributed' populations. Varieties which were least similar to 4's were at the greatest advantage. Correspondingly, the variance of the population increased as the frequency of 4's diminished.

Morph 4 was at a relative disadvantage because it was effectively common. It was not eliminated from the population - at least within the period of study. One reason for this was that the effects of conditioning decreased with time as the birds discovered the other types of bait. Elimination of morph 4 might have occurred if, for example, it had been more conspicuous than the other varieties.

Cain et al. 1960 and Turner 1961 have in fact suggested that disruptive selection by predators could act to eliminate conspicuous phenotypes such that the optima come to resemble particular elements of the background. Certainly a number of species do appear to exhibit such 'cryptic polymorphism' (Cain et al. op.cit.) and in many cases some morphs are green and others, brown.

Many terrestrial environments, for example grassland, woodland, mixed herbage, etc., are essentially composed of a complex medley of numerous shades of green and brown. These colours appear in many polymorphic species inhabiting such habitats. Cases in point are: the caterpillars, pupae and imagoes of certain Lepidoptera, for example the larvae of Geometron papilionaria L. (Poulton 1884); various species of Mantidae (Edmunds 1972); the nymphs and imagoes of numerous Acrididae (Byrne 1967, Owen 1966a, personal observations); the earthworm Alloobophora chloritica L. (Satchell 1967); the East African molluscivorous land snail Edentulina obesa (Gibb.) (personal observations); numerous tree-frogs, e.g. Hyla regilla (Resnick and Jameson 1963), various Hyperolius species (Schlitz 1967, 1971); the chameleon Chamaeleo bitaeniatus (Ogilvie and Owen 1962). Many other examples could be mentioned.

Variation even in Cepaea is based on green versus brown, for the yellow morphs often appear green when the snail is in its shell. Cain et al. (1960) were first to point out that the morphs of C. nemoralis seem to resemble components of the background.

Polymorphic species inhabiting other types of habitat also show such correlations between the colours of the morphs and the background. Safriel (1970) discovered that the morphs of the

intertidal gastropods Nerita forskalii Réclius and N. polita Linné resemble the colours of the pebbles in their environment. A similar case has been made for the limpet Acmaea digitalis (Giesel 1970).

The morphs of certain species therefore tend to resemble elements of the habitat and this might imply that they are kept visually distinct by disruptive predator selection. Giesel (1970) has obtained indirect evidence that such a situation exists in Acmaea digitalis.

It is doubtful whether much of the selection in experiment 4 was related to the diversity of the background because none of the nine varieties appeared to be the same colour as any particular component and they seemed equally conspicuous. However the experimental design could easily be modified to test the maintenance of the distinctness of 'cryptic morphs'. Such a line of enquiry would surely be profitable.

(ii) Maintenance of variability

Mather (1955) has emphasised that one of the conditions that must be fulfilled for disruptive selection to maintain a polymorphism is that each optimal phenotype should be an effective part of the environment of the others. Sex is an obvious example; male and female phenotypes must occur together in the same population. In mimetic polymorphism the success of each morph depends on the frequencies of the others, for the commoner the mimic the more likely it will become associated with palatability. Likewise, in apostatic polymorphism, the selective value of each phenotype is assumed to be inversely related to its frequency.

Polymorphism in a palatable species will be maintained by a 'disruptive' predator only if the selection is frequency-dependent. Experiment 4 showed that the birds tended to take the common (familiar) colour, thus affording protection to the rarer forms, and suggesting that the selection had an apostatic component. However, frequency-independent brown preferences and the diversity of behaviour hindered the detection of apostatic selection during the experiment's later stages. It is clearly essential to carry out further experiments to test whether apostatic selection can indeed act on strictly polymorphic (as opposed to dimorphic) populations as is suggested by the work of Popham (1942, and discussed on pp. 42-44 of this thesis).

6. SUMMARY

To reiterate, the main findings were:

- (a) Searching images can be very specific.
- (b) As in other experiments, blackbirds (with one exception) and songthrushes preferred brown baits.
- (c) The birds were very variable in behaviour.
- (d) En masse, they acted in a manner that may be capable of promoting polymorphism in a prey species.

APPENDIX D: TABLE 54

'Normal distribution' experiment 4: data
for predation over every three generations
by blackbirds E, J, K, L, M, and two
songthrushes.

Numbers of baits taken over every three (or two) generations by individual blackbirds (E, J, K, L, M) and the two songthrushes (T's).

Generations 0 - 2

Birds	E	J	K	L	M	T's	Totals
0	0	0	0	0	0	2	2
1	0	1	2	2	0	3	8
2	5	1	4	6	0	5	21
3	14	3	9	6	2	8	42
4	10	23	6	10	1	11	61
5	5	10	5	2	1	11	34
6	4	0	1	3	1	8	17
7	0	0	0	1	0	0	1
8	0	0	0	1	0	0	1
Totals	38	38	27	31	5	48	197

Generations 3 - 5

Birds	E	J	K	L	M	T's	Totals
0	2	0	0	1	0	0	3
1	2	1	1	3	0	3	10
2	4	1	1	4	0	1	11
3	7	6	9	7	0	10	39
4	8	6	6	7	0	10	37
5	8	28	7	7	1	3	54
6	4	9	1	5	0	8	27
7	4	2	2	1	0	1	10
8	1	0	0	2	0	1	4
Totals	40	53	27	37	1	37	195

Generations 6 - 8

Birds	E	J	K	L	M	T's	Totals
0	1	0	2	1	1	1	6
1	3	0	0	3	2	12	20
2	6	2	3	3	2	12	28
3	11	5	7	6	3	14	46
4	9	5	6	6	4	7	37
5	3	15	7	2	2	8	37
6	3	14	3	2	0	3	25
7	3	12	0	4	0	6	25
8	0	0	1	0	0	0	1
Totals	39	53	29	27	14	63	225

Generations 9 - 11

Birds	E	J	K	L	M	T's	Totals
0	2	0	0	0	1	1	4
1	2	0	4	1	1	4	12
2	8	0	5	8	4	8	33
3	7	1	8	4	5	14	39
4	7	7	3	5	2	14	38
5	3	26	5	3	3	9	49
6	1	12	2	4	0	8	27
7	0	4	3	2	0	5	14
8	0	1	0	0	3	1	5
Totals	30	51	30	27	19	64	221

Generations 12 - 14

Birds	E	J	K	L	M	T's	Totals
0	1	0	1	1	1	3	7
1	0	2	1	2	3	3	11
2	3	0	4	1	10	7	25
3	9	1	5	5	8	7	35
4	2	4	3	8	7	6	30
5	5	25	5	9	6	10	60
6	1	12	2	1	6	5	27
7	1	6	0	1	1	3	12
8	1	1	0	3	2	0	7
Totals	23	51	21	31	44	44	214

Generations 15 - 17

Birds	E	J	K	L	M	T's	Totals
0	1	0	1	3	0	0	5
1	5	1	6	5	8	1	26
2	4	2	2	6	5	6	25
3	6	7	5	4	11	3	36
4	1	8	3	3	1	18	34
5	4	10	4	4	3	2	27
6	2	5	1	3	2	7	20
7	3	6	2	2	1	4	18
8	1	1	0	1	1	4	8
Totals	27	40	24	31	32	45	199

Generations 18 - 19

Birds	E	J	K	L	M	T's	Totals
0	1	0	3	2	1	2	9
1	3	2	2	1	2	5	15
2	3	1	9	6	3	5	27
3	6	2	10	3	3	3	27
4	0	3	0	1	1	1	6
5	2	11	3	2	2	4	24
6	0	2	2	2	0	4	9
7	3	4	5	2	0	0	14
8	2	3	0	1	0	0	6
Totals	20	28	34	20	12	23	137

CHAPTER X GENERAL DISCUSSION AND CONCLUSION

CHAPTER X GENERAL DISCUSSION AND CONCLUSION

The results have been discussed in full in each of the six preceding Chapters. This final section attempts to bring together the several lines of thought which the work has invoked. The findings will be used as a basis for discussing apostatic selection in natural populations and I shall stress likely areas of future research. Before we do this we should justify the experimental set-up as being realistic of a natural situation, first from the point of view of the predator and second from the point of view of the prey.

1. WILD PASSERINES AS PREDATORS OF POLYMORPHIC SPECIES

My experiments have shown that certain wild passerines, notably the blackbird Turdus merula, tend to behave in a manner that is capable of actively maintaining a colour polymorphism in a prey species. It could be argued that the results are meaningless, simply because these birds do not normally eat polymorphic prey. However the evidence is to the contrary.

The blackbird, for example, is very catholic in its choice of diet (Witherby et al. 1938, Collinge 1941, Snow 1958). Its favourite items include earthworms and caterpillars (Snow 1958) and both of these groups contain polymorphic species, some of which are even dimorphic for green versus brown (see p. 252). In addition the remains of snails have been found in the stomachs of blackbirds (Collinge 1941) although they "lack the nervous equipment for hammering [snails] against an anvil" (Morris 1954).

It is probable that snails are taken when they are small and weak (Morris op.cit.)¹. This would include the young of many polymorphic species (Cepaea, Arianta, etc.). If blackbirds (and indeed other avian species) take appreciable numbers² of young, e.g. Cepaea, it is possible that apostatic selection acts early in the snail's life-history and not later, as has been generally supposed (Clarke 1962a,b). Despite the number of papers written on Cepaea, ecologically we have but scratched at the surface. Other polymorphic species have been even less investigated.

Even if the blackbird is not an important predator of polymorphic species it is closely related to one that is - the songthrush. Both species are essentially ground-feeders and share a similar diet, with the obvious exception that the songthrush alone has developed the ability to break large snails. The behaviour of bait-eating blackbirds may have direct implications to the behaviour of the Cepaea-eating songthrush. The few songthrushes encountered during the study certainly did not differ noticeably from blackbirds in their responses to the baits. Admittedly, songthrush T (of the experiments in Chapters VII and VIII) had the strongest brown preference of all the individuals investigated, but this may have been a chance result (p. 158).

The other predators in the experiments (see Table 1, p.52) also undoubtedly encounter polymorphic prey in nature (e.g. for Parus spp. see the work of Den Boer (1971), described below, p.265).

¹Morris (1954) also points out that blackbirds steal large snails from thrushes, at the critical moment when 'hammering' has ended and the snail has been extracted. This method has little relevance in the present context.

²Witness Gibb's (1956) remarkable data for the quantities of Littorina sp. consumed by a single rock pipit Anthus spinoletta.

Starlings and house sparrows featured prominently in some experiments. These birds are 'social feeders' and it is possible that they are more efficient 'apostatic' predators than Turdus spp., because 'social facilitation' may ensure that nearly all the individuals concentrate on the profitable, common varieties (see pp. 188-190).

2. BAITS AS NATURAL PREY

It could also be argued that because the prey were artificial the birds responded to them in an artificial manner. However the evidence, as outlined below, does not give much support to this possibility.

(a) The main colours of the prey, green and brown, are typical of many palatable animals, including certain polymorphic species.

(b) It is possible that the birds were reacting abnormally because the baits did not taste particularly 'animal-like'. The baits however contained a high proportion of animal fat. In addition, J.N.M. Smith has informed me that blackbirds show no significant preference when given a choice between lard-and-flour baits either containing or not containing a meat-extract ingredient.

(c) Although the baits were immobile, many polymorphic species may also rely on immobility as a primary line of defence (see below). In any case, the baits were not completely without behaviour, because their spatial arrangements were altered periodically.

(d) The usual density of the baits, two per square metre, is certainly comparable with the densities of natural polymorphic

prey; populations of certain species occur at even higher densities (see below).

(e) Casual observations suggested that the hunting patterns of blackbirds and thrushes searching for baits were little different from when searching for small insects or worms, a conclusion that is given support by the work of J.N.M. Smith¹ (personal communications).

(f) Most important, the birds were feeding in their normal surroundings and were not subjected to the potentially distorting rigours of captivity.

3. EVIDENCE FOR APOSTATIC SELECTION

Chapter II examined the then existing evidence for apostatic selection and posed three basic questions concerning the evidence for (a) conditioning to a specific prey, (b) specificity of conditioning, (c) apostatic selection. Some answers can now be provided in the light of the experiments.

(a) Conditioning to a specific prey

The keystone to the hypothesis of apostatic selection is the assumption that predators, under certain conditions, hunt morphs on the basis of specific searching images. Evidence has been presented (mainly in Chapters V and IX) in support of this contention: birds can be trained to search for familiar baits.

(b) Specificity of conditioning

The experiments described in Chapter IX show that the searching image can be very specific when birds are trained on one

¹Smith's work has now appeared as a D.Phil. thesis, University of Oxford (1971), but this has not been seen by the author at the time of writing.

colour and then presented with a choice between the familiar and a similar unfamiliar colour.

(c) Apostatic selection

Proof of searching image behaviour is not proof of apostatic selection. If searching images are readily acquired for rare morphs selection will act to eliminate variability. Predators must preferentially search for common varieties. The training experiments of Chapters V and IX showed that this occurs when birds are familiarized with one colour. All the birds acquired searching images specific to the familiar, i.e. 'common' morph. But this is unlikely to happen in nature. Some individuals may build up searching images from chance encounter with rare varieties, and this contention is supported by the results from the low-density 9:1 experiments (Chapters VI-VIII).

The responses of individual predators thus tend to be more diverse than might be expected and other factors in addition to the one mentioned may also contribute to the heterogeneity (Ch. VIII). It is wrong to discuss apostatic selection on the assumption that individuals of a given predator species are homogeneous in their responses. This notion is implied in the writings of various workers (e.g. Clarke 1962a, Elton and Greenwood 1970, but not Cook 1965). The important criterion is that the overall response of the predators should be apostatic, as seems to have been the case in my 9:1 experiments.

A further point needs to be stressed. In his original paper on the subject, Clarke 1962a, p.59) defines apostatic selection as selection by predators that confers an advantage to "phenotypes that stand out from the norm". He means selection that favours

morphs which are numerically rare. This is an over-simplification, for the situation may often be complicated by frequency-independent selection by predators. In my 9:1 experiments, the Turdus species on average preferred browns, and Arnold (unpublished) found that his songthrushes also have frequency-independent preferences for certain morphs of Cepaea. Thus, for example, a morph that is 'fairly common' numerically may be 'very common' to a predator which for some reason has a strong preference for its colour-pattern. If apostatic selection were acting, this morph would be at a greater relative disadvantage than would be expected on the basis of its apparent frequency. Hence it is important that analysis for evidence of apostatic selection attempts to take account of frequency-independent preferences. Elton and Greenwood (1970) have provided two mathematical models for estimating the apostatic component of selection in situations where data have been obtained from a number of populations containing different proportions of two morphs of a species.

A definition of apostatic selection should therefore stress that a 'rare' morph is not necessarily numerically uncommon. For example:

apostatic selection is selection that confers an advantage to phenotypes which to the predator appear to stand out from the effective norm.

The next logical step is to extend the research to observe how predators respond to natural polymorphic prey. In fact the work of Arnold (see p. 46) supports the argument that songthrushes prey apostatically on Cepaea. The birds were not observed

continuously but his results imply that they were using morph-specific searching images. Recently, Den Boer (1971) has obtained some promising results for captive tits Parus major and P. ater feeding on dimorphic (green versus yellow) caterpillars of the pine looper Bupalus piniarius (L.). He has shown that tits can be conditioned to green larvae such that in a choice situation this morph is preferred (compare with conditioning experiments, Chapter V). Since the green morph outnumbers the yellow by 1 to 500, Den Boer (op.cit.) suggests that apostatic selection is maintaining the polymorphism, even though the yellow appear more conspicuous on pine needles, the normal habitat of the larvae.

Den Boer's work is perhaps the first direct proof that predators hunt morphs by specific searching image. An axiomatic feature of a species showing apostatic polymorphism is that some or all of its major predators could hunt by searching image. At present, however, we do not know to what extent searching image behaviour occurs in the Animal Kingdom. My results and those of others (e.g. Tinbergen 1960; Croze 1970; Dawkins 1971a; Miller, in preparation) apply to birds, which are probably often important predators of polymorphic prey. Similar behaviour may occur in other vertebrates (reptiles and amphibia) possessing colour-vision, but these Classes have not yet attracted much attention. Colour-blind mammals may select apostatically on the basis of tone, or even smell (see p. 38). There is some evidence (Landenberger 1968) that invertebrates (starfish) also tend to hunt for common prey and this would have important consequences if such selection were shown to act on polymorphic species.

O'Donald (1968) has discovered that glow-worms are certainly capable of distinguishing between various morphs of Cepaea nemoralis. The possibility of apostatic selection by invertebrates clearly warrants further investigation.

4. CONDITIONS FOR APOSTATIC POLYMORPHISM

Accepting that the experimental design is representative of a natural situation, we can now use the results as a basis for discussing the conditions favourable to polymorphism maintained by apostatic selection. It should be immediately pointed out that proof of apostatic selection in a natural population does not necessarily imply that the polymorphism is so maintained. The effects of frequency-dependent selection could be swamped by selection that is independent of the frequency of the phenotypes. However, Cook (1965) has calculated that the fraction of individuals eaten by predators has only to be of the same order of magnitude as a frequency-independent coefficient which is tending to eliminate the variability. It must also be realised that proof of apostatic selection does not rule out the possibility that other mechanisms are helping to maintain the polymorphism.

My experiments were not planned specifically with the aim of testing the conditions for apostatic selection. As we have seen, many of the properties of the predator-prey system were kept as constant as possible throughout the work. Nevertheless the research has yielded some promising clues that could be followed up in the future.

For our present purposes we shall assume that polymorphic species are liable to attack by predators that hunt by searching

image. In a discussion of the conditions most likely to favour apostatic selection we would like to know the relationship between the 'apostatic disproportion' (Greenwood 1969) and the various properties of the prey.

The apostatic disproportion is a measure of the strength of apostatic selection. For a dimorphic species where morph A is rarer than morph B, and assuming that the morphs are equally attractive (in terms of palatability, conspicuousness, etc.), the apostatic disproportion is the cross-product ratio:

$$\frac{\text{density of A} \times \text{number of B eaten}^1}{\text{density of B} \times \text{number of A eaten}}$$

This term will be greater than unity if selection is apostatic. Its magnitude will partly depend on the relative frequencies of the morphs; the rarer is morph A, the greater its relative selective advantage and hence the greater the disproportion. It would be a straightforward matter to determine how the magnitude of the apostatic disproportion is related to the relative frequencies of the morphs. The heterogeneity within my experiments forced me to confine attention to the situation at low densities when one morph is nine times as common as the other. Future work should include the presentation of populations containing the two morphs in various proportions.

The magnitude of the apostatic proportion is likely to depend not only on the low frequency of the rare morph but also on the properties of the species as a whole. Conditions for apostasis should be such that searching images are acquired for common morphs and not for rare morphs (Clarke 1962a). This means,

¹cf. cross-product ratio used in 9:1 experiments, e.g. p.104.

in effect, that the number of individuals encountered per unit time by a given predator should be neither too high nor too low. If the prey are encountered too often, searching images are likely to be acquired for rare varieties and, in addition, selection may be such as to favour a mixed diet, and may therefore tend to randomness (Tinbergen 1960). If the prey are encountered too rarely, searching images are unlikely to be acquired for any morph.

The 'risk of encounter' will in part depend on the properties of the predator; for example, its state of hunger, the randomness of its hunting pattern, its visual acuity, etc. These factors were not investigated in the present experiments because the birds were in their normal surroundings and it was not possible to observe very many aspects of their behaviour at the same time. Here we shall discuss the factors affecting the risk of encounter mainly in terms of the properties of the prey species as a whole: i.e. the density, conspicuousness, and palatability of the prey.

(a) Density

Clarke (1962a) suggests that apostatic polymorphism will be favoured only when the prey is 'fairly uncommon' such that rare morphs are encountered infrequently. At too high a density, monomorphism may result from searching images being acquired for rare morphs, and at too low a density monomorphism may again result because searching images are not acquired for even common varieties. Greenwood (1969) has arrived at a similar conclusion by using a wider, mathematical, argument (see below).

The investigation of the relationship between the apostatic disproportion and density was outside the scope of my experiments. Apostatic selection was observed when the baits were at a density of 2 per square metre on grass and soil backgrounds. In the absence of other experiments, we do not know whether this density is 'low', 'intermediate' or 'high'. However, at some higher density, selection must tend to randomness, for at maximum density the rarer morphs were preferred (Chapter IV, see also Allen 1972). It seems that at very high prey densities predators tend to behave in a manner that is capable of actively eliminating variability. It need hardly be pointed out that the relationships between apostatic, stabilizing selection and density could be easily studied with baits and wild birds.

There is some indirect evidence that the intensity of apostatic selection in my 9:1 experiments would be exceeded if the work was repeated at densities higher than 2 baits per square metre. Owen (1965a, b) has collected samples of Limicolaria martensiana from Uganda and has shown that polymorphism (as measured by the number of morphs) is directly related to density. The populations that were most polymorphic were those containing over 100 snails per square metre. This implies that apostatic selection is directly related to density, at least in the samples examined. It is possible that populations of very high densities would tend towards monomorphism (cf. Clarke 1962a). Similar results have since been reported by Smith (1971) for the West African bivalve Donax rugosus.

Greenwood (1969) has stressed the importance of determining

the relationship between the magnitude of the apostatic disproportion and the density of the prey. Owen (1965a, b) explains the Limicolaria results (see above) on the basis of the assumption that the relationship is variable such that the disproportion is highest at high densities. Greenwood (op.cit.) points out that the data can also be interpreted by postulating that the disproportion is for example, independent of density.

He refers to Holling (1965) who has produced a mathematical model, supported by experimental evidence, which predicts that the proportion of deaths due to a vertebrate predator will be highest at intermediate densities, and lowest at high and low densities. For simplicity the overall selection due to deaths from other causes may be assumed to be independent of density. It is also likely to be independent of frequency and will lead to decrease in variability if acting alone. If the disproportion is independent of density, then apostatic selection will be relatively more important at intermediate densities than at high or low densities.

There is a corollary to the hypothesis that in palatable species selection by predators tends to promote polymorphism at intermediate densities and monomorphism at high and low densities. The model equally applies to variation between two or more palatable monomorphic species. My brown and green baits for example could be regarded as two separate species instead of two morphs of the same species. At intermediate overall densities apostatic selection may favour mutations that accentuate the dissimilarities of colour-pattern so that the two species tend to diverge in appearance (Clarke 1962a, Holling 1965). From the training experiments in Chapter IX we can conclude that

these differences do not have to be very large, particularly if one species is relatively more common than the other.

When both species are rare, searching images are unlikely to be acquired for either, but when the overall density of the two species is high, there will be "no necessary divergence and indeed there may be convergence" (Clarke 1962a, p. 62). In fact this idea had long been foreshadowed by Wallace (1889) who suggested that a scarce edible species can closely resemble a sympatric abundant edible species and thus gain some freedom from predation. Van Someron and Jackson (1959) have proposed a similar explanation for parallelism of colour-pattern in African butterflies.

The essence of such 'safety in numbers' (Van Someron and Jackson, op.cit.) is that at high densities, predators quickly become satiated so that the proportion of prey destroyed decreases after a certain density has been reached (Holling 1965). The proportion eaten in any one species will therefore be less than in the absence of 'mimicry'. The results from the maximum density experiments (Chapter IV) suggest an additional mechanism for the evolution of such 'mimicry' among palatable species.

(b) Conspicuousness

The risk of encounter will partly depend on the 'effective density' of the prey species, that is the average distance from which a particular predator can detect one of the prey. The smaller the 'direct detection distance' (Croze 1967, 1970) the lower the risk of detection. The properties of the prey that affect the direct detection distance can be discussed under the collective term 'conspicuousness' and will include such factors as coloration,

size, behaviour and environment.

Many colour polymorphisms are 'cryptic' (Cain, King, and Sheppard 1960) in the sense that the colour-patterns of some or all of the morphs appear to match components of the background. Concealing coloration will reduce the direct detection distance and so reduce the chances of a naive predator finding a given individual. To be effective, concealing coloration must be associated with 'cryptic' behaviour (Cott 1940) to ensure that the prey remains motionless in situations where most likely to be attacked, only fleeing at the last possible moment, if at all. Many polymorphic species exhibit cryptic behaviour. Indeed the habit may be a prerequisite for apostatic selection. It is impossible to give a comprehensive list, but polymorphic snails (e.g. Cepaea), treefrogs (e.g. Hyperolius), isopods (e.g. Sphaeroma), grasshoppers (e.g. Homorocoryphus) are all characterised by spending many of their diurnal hours motionless in situations where they are exposed to predators. Examples in birds also seem to fit the rule. Polymorphism is commonⁱⁿ herons (Ardeidae) and it is well-known that these birds stand motionless for hours as they wait for prey¹. The polymorphic bush-shrikes (Malaconotus spp.) are notoriously skulking birds of the African bush (Mackworth-Praed and Grant 1955, and personal observations).

Obviously if a prey species is too concealed then the intensity of predation may not be sufficient to allow for apostatic polymorphisms. One would not expect to find such variation in organisms that spend all their time underground, for example. On the other hand

¹Murton (1971c) has made a different interpretation of polymorphism in herons but he does not satisfactorily explain how the variation is maintained.

conspicuous palatable species which rely on mobility for their first line of defence are likely to be noticed, in the first instance, by their behaviour. Selection for apostasy is unlikely to occur under such conditions and this might explain why non-mimetic polymorphism is uncommon in such groups as butterflies and many birds.

The conspicuousness of a prey species will also depend on the nature of the environment: the risk of encounter may be expected to be less in dense habitats than in open ones. In fact Cain and Curney (1968) have shown that thrush predation on a population of Cepaea nemoralis is of greater intensity in tussocky grass than in neighbouring nettle patches. A dense habitat will lower the intensity of predation in a number of ways. First, it will act as a physical barrier to the predator, hindering movement. Second, it will render the prey difficult to see, because there are more distracting components in the background vegetation. Third, it will enable a greater area for dispersion of the population. If the prey are prone to climb (and Clarke, 1962a, has suggested that polymorphic snails may tend to climb more than monomorphic species) then predators will have to search in a vertical plane as well as in a horizontal plane. Taking the last factor into consideration we may now realise that a density of 100 Limicolaria snails per square metre of thicket may in effect be a good deal lower.

The effect of coloration on the magnitude of apostatic selection could be investigated by repeating my low density 9:1 experiments with either more cryptic or more conspicuous morphs. Care would have to be taken to ensure that natural colour preferences are accounted for. An even more intriguing study would be to repeat the experiments with greens and browns but in more 'difficult' or more 'easy' environments.

(c) Palatability

The risk to a polymorphic species would be decreased if it is 'slightly distasteful' (Clarke 1962a). As Clarke points out, Cepaea may be slightly distasteful, for thrushes eat the snails in large numbers only when alternative food is scarce (Sheppard 1951, Goodhart 1958, Wolda 1963, Davies and Snow 1965). The same remarks probably apply to other polymorphic snails and slugs. A species that is too distasteful may be expected to become monomorphic through the evolution of an aposematic colour-pattern, but certain distasteful species are in fact polymorphic (e.g. the South American butterflies Heliconius melpomene, H. erato and H. doris, Turner 1965, 1968; the African butterflies Danaus chrysippus and Acraea encedon, Owen 1970). It is possible that even these so-called 'protected' species suffer enough deaths from predation to allow for the maintenance of variability by apostatic selection; although, as Turner (1968) points out with regard to Heliconius melpomene and H. erato, other mechanisms may be responsible.

In my experiments the palatability of the baits relative to alternative available natural food was not measured, but they were obviously very attractive because they were usually taken in preference to other prey in the plots. Hence 'tasteful' prey were actually intrinsic to the achievement of apostatic selection. This does not detract from the possibility that apostasis might have been more pronounced had the baits been less palatable. Further experiments should be carried out with baits of varying degrees of palatability.

There are in fact some ^{polymorphic} species which may be thought to be positively palatable to predators; obvious examples occur in the

Acrididae, such as the African edible grasshopper, Homorocoryphus nitidulus. But the important criterion is the palatability of the species relative to other prey items of the 'apostatic' predator. The species may be eaten but rarely if it is low on the predator's palatability spectrum.

5. TYPES OF APOSTATIC POLYMORPHISM

Non-mimetic colour polymorphisms have long excited the attention of research workers. Yet most efforts have concentrated on the genetics and associated ecology of the organisms; the actual visual appearance of the variation has been neglected. There is much work to be done, for example, on the relative conspicuousness of the morphs and, of course, as to whether they can instill specific searching images in predators. There is also much to be gained from a study of colour-polymorphism on a comparative basis, but on a much wider scale than was attempted by Owen (1963b). I shall now endeavour to present a brief interpretation, necessarily preliminary and speculative, of the kinds of apostatic polymorphisms that may exist in the Animal Kingdom.

We would be on safest ground when considering a species dimorphic for green versus brown and known to be subject to attack from avian predators! In fact, such prey animals are probably not uncommon and some examples have been given in Chapter IX (p. 252). To illustrate the point, consider the green-brown dimorphism which occurs in the larvae of many Lepidoptera. These caterpillars usually live on trees and bushes and are

doubtless eaten by various species of birds. Here, then, is a situation that is similar to the one in my 9:1 and training experiments. It is very tempting to suggest that apostatic selection maintains the dimorphisms of such larvae. That this may indeed be the case is supported by Den Boer's (1971) findings that birds can acquire searching images for the green and yellow morphs of the larvae of the pine looper (see above, p. 265).

On the basis of the results from Chapter VIII ('trimorphic' experiment, 2.3d) and Chapter IX ('normal distribution' experiments), we can extend the argument to cover green-brown polymorphism where more than two morphs are involved. This applies to many Orthoptera—for example, the grasshopper Homorocoryphus nitidulus has six morphs, three based on modifications of a green body colour, and three based on brown (Owen 1965c, 1966a). Cepaea might also be regarded essentially as having green and brown morphs (p. 252).

The species mentioned above and on page 252 live in habitats where green and brown predominate in the background and it is difficult to escape the conclusion that the morphs 'mimic' these components. This hypothesis, first mooted by Poulton (1890), does not detract from the argument that apostatic selection maintains the polymorphism, but provides an additional method for maintaining the discontinuity of the variation. This reasoning can be extended to polymorphic species in other types of habitats where the morphs also appear to mimic elements of the background (page 253).

Clarke (1962a, 1969) and Owen (1963b, 1966a) have stated that some morphs of certain polymorphic species (Cepaea and Limicolaria) do not seem to resemble any colour pattern in the habitat. This belief may be partly due to a misunderstanding of the principles of

concealment, which have been so well detailed by Cott (1940). To the well-trained, scarcely naive human predator, a mid-banded Cepaea, a semi-streaked Limicolaria, or a yellow-striped Sphaeroma may indeed appear highly conspicuous on any background. But to a lowly vertebrate predator this may not necessarily be the case. We can do no better than to quote from Cott (op.cit., pp.48-49) himself: He refers to disruptive coloration:

"Even the simplest disruptive patterns tend to hinder recognition and so make for concealment...For example, the East African Rana adspersa a large frog whose general colour-scheme is a patch-work of subdued earthy-browns and olive-greens - wears on its back a conspicuous yellow stripe extending from the snout right along the middle of the back...So far from drawing attention to the animal, however, the effect of this stripe is quite the reverse. In the first place, the yellow line - which, of course, in itself bears no resemblance whatever to its wearer, but rather suggests to the casual glance a twig or blade of grass - stands out from the back and catches the observer's eye. Secondly, by providing a strong incident of colour, it serves to flatten by contrast the less-defined half-tones by which the real form of the frog is differentiated from its surroundings. In the third place, it serves to bisect the form of the frog, so that the eye of the enemy is actually presented with a configuration of two half-frogs - which look very different from one whole one - and as likely as not the brain behind the eye will fail to join them together in recognition!"

In other words such a prey animal gains survival value by virtue of its conspicuous disruptive stripe (or other disruptive marking). The effect is enhanced when some of the component patterns harmonise with the background while others strongly contrast with it (Cott, op.cit.). Thus certain parts of the prey stand out whilst others merge with the background, and consequently the real appearance of the prey cannot be readily determined.

I suggest that some of the so-called 'conspicuous' morphs of certain species are disruptively coloured. In fact disruptive

coloration may occur frequently in polymorphisms. For instance, of the morphs of Sphaeroma rugicauda (West 1964) I would class all but one (the uniformly coloured 'grey' morph) as disruptively patterned. Other examples abound in hemiptera, snails, grasshoppers and frogs.

Disruptive coloration and apostatic selection may be compatible concepts. A contrasting disruptive pattern will render the prey inconspicuous to a naive predator. But if the predator accidentally detects the animal then it has only to latch on to the conspicuous component of the pattern in order to find more prey. The acquisition of the appropriate searching image should then be rapid for, once recognised, the patterns tend to be very noticeable. Rarer phenotypes would then be favoured. Thus, through the agency of apostatic selection, a given environment may be able to support more than one type of disruptive pattern within a species. In addition some morphs (e.g. 'grey' of Sphaeroma rugicauda, certain varieties of Cepaea) may bear a 'general colour resemblance' (Cott 1940) to the background. Finally, some morphs may be truly 'apostatic'. For even when disruptive coloration is taken into account there are still some varieties which appear to be conspicuous in any background - for example, bright pink unbandeds of Cepaea (Clarke 1962a, 1969), certain morphs of Philaenus and Limicolaria (Owen 1963b). Such forms may indeed be maintained within populations by virtue of their difference from the norm. In some species (e.g. Cepaea) only the minority of the morphs may be conspicuous; in other species (e.g. Limicolaria) the opposite may be the case.

It will be realised that disruptive coloration effectively

increases the visible differences between the morphs. A predator hunting Sphaeroma rugicauda is likely to acquire a 'Sphaeroma-shaped' searching image only when it has become familiar with greys. At other times it is likely to be searching specifically for 'T-shaped black patches' (the pattern morph), 'narrow bright yellow stripes' (the yellow morph), 'wide brick-red stripes' (the red morph), etc. The morphs therefore effectively differ in their shape, as well as colour.

In some polymorphisms in non-mimetic species all the morphs are conspicuous. The variation in many of these species has been described as 'massive' (Moment 1962). This occurs in animals such as the butterfly clam Donax variabilis, the brittlestar Ophiopholis aculeaton, the coelenterate Cerianthus americanus. In these species it is rare to find two individuals that look alike and Moment suggests that it is the variation per se which is adaptive because it makes it impossible for predators to form specific searching images. Croze (1967, 1970) presents experimental evidence in support of this view. However, as mentioned previously such a situation could only have evolved through the action of apostatic selection: 'reflexive' polymorphism may be the final stage of apostatic polymorphism.

It is possible that massively variable species tend to live in relatively uniform habitats such as sandy beaches - this is certainly true of Donax. These environments bear few components which can be mimicked. For a palatable species exposed to predators and unable to camouflage itself effectively, massive polymorphism might be the only answer.

Even from the above outline we can conclude that the types of supposed apostatic polymorphism are many and varied. There are species

which all the morphs are coloured for concealment, whether by general colour resemblance or by disruptive coloration. Other species possess morphs which seem to be genuinely conspicuous. In still other species all the morphs appear conspicuous and the diversity is often massive. These categories are by no means exclusive for there may be all types of polymorphism from 'cryptic' to conspicuous. The classification could be made more complicated by bringing in such factors as environment, degree of polymorphism, palatability, etc., but in the absence of facts there is little point in further speculation at present. Colour polymorphism has yet to be studied on a comparative basis.

6. CONCLUDING REMARKS

In 1962 Clarke used the term 'apostatic polymorphism' for the first time. His choice of adjective may then have appeared somewhat presumptuous because the experimental evidence for apostatic selection was undeniably scanty. But the last ten years have seen the steady accumulation of data. The work in this thesis represents a concerted attempt to test apostatic selection. It has, I hope, provided strong support for the hypothesis.

Other workers (e.g. Croze 1970; Dawkins 1971a; Miller, in preparation; Shutt, unpublished) have obtained comparable results with birds and artificial prey. Nevertheless, as we have seen in the present Chapter, there is still much to be learned from birds and baits. The field studies of Arnold (unpublished) and Den Boer (1971) are promising pointers to future work and the time is ripe for more direct observations of predators feeding on natural polymorphic prey species.

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APPENDIX E : PUBLISHED PAPERS

ALLEN, J.A. and CLARKE, B. 1968. 'Evidence for apostatic selection by wild passerines'. Reprinted from Nature, 220: 501-502.

AND

ALLEN, J.A. 1972. 'Evidence for stabilizing and apostatic selection by wild blackbirds'. Reprinted with corrections of publisher's errors, from Nature, 237: 348-349.

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Evidence for Apostatic Selection by Wild Passerines

It has been suggested that predators concentrate on common varieties of prey, and tend to overlook rarer forms even if they are obvious^{1,2}. Within a prey species this apostatic selection could act to maintain a balanced polymorphism^{2,3}. The selection would then be dependent on frequency in the sense that the selective value of each phenotype would vary inversely with its frequency^{4,5}. Direct evidence of such selection has been obtained from experimental studies of predation by fish², and there is indirect evidence of similar selection by birds^{1,2,6}. Ground-feeding passerines are important predators of many polymorphic insects and molluscs, and we report here some preliminary experiments designed to investigate their behaviour when presented with artificial dimorphic prey⁷.

We used wild birds in their normal surroundings. The most frequent species were blackbirds (*Turdus merula* L.), house sparrows (*Passer domesticus* (L.)), dunnocks (*Prunella modularis* (L.)), starlings (*Sturnus vulgaris* L.) and robins (*Erithacus rubecula* Hart.). The prey were cylindrical baits (0.7 cm long $\times$ 0.7 cm in diameter), made of flour and lard in the proportion 5 : 2 by weight. They were coloured green or brown by the addition of edible dye (11 cm³ dye to 1,000 g of mixture). In other respects, including hue and brightness⁸, the baits were apparently identical. We find no evidence of differences in taste.

The first series of experiments involved populations of baits in which one colour was nine times commoner than the other. In August 1966 a square grid of 100 one-metre squares was marked out on the lawn of the Department of Zoology at Edinburgh. Within it, 180 green and twenty brown baits were distributed at random, two baits in each metre square. To the human eye the browns were slightly more conspicuous. The spatial distribution of baits was changed each day. During the experiment the grid was under continuous observation, and a record was kept of the numbers of baits taken by the birds at each visit. Frequent replacement of baits ensured that the 9 : 1 ratio was kept constant. After seven days of predation, the experiment was repeated with a population of 20 greens and 180 browns. The daily totals of baits eaten are shown in Table 1. Below the grand totals are given the expected numbers based on the assumption that there is no selection.

The blackbirds and starlings took more browns than expected in both experiments. Dunnocks and house sparrows, on the other hand, took more greens in the first experiment and more browns in the second. It is clear from these results that the birds exercised visual selection,

Table 1. DAILY TOTALS OF BAITS TAKEN: GRASS BACKGROUND

Experiment 1

180 greens : 20 browns

Date	Hours of observation (BST)	Blackbirds		Observed predation				H. Sparrows	
		(6+)		Starlings		Dun-		(many)	
		G	B	G	B	G	B	G	B
30.7.66	9.03-12.00	2	0	—	—	—	—	—	—
1.8.66	10.30-18.15	61	9	0	1	1	0	—	—
2.8.66	8.30-10.30	71	22	—	—	4	0	—	—
3.8.66	9.20-15.15	71	17	—	—	5	0	10	1
5.8.66	10.30-17.05	45	11	—	—	14	0	86	2
6.8.66	5.09-7.51	69	15	—	—	—	—	14	0
7.8.66	16.06-18.10	35	12	20	2	—	—	57	0
Grand totals		354	86	20	3	24	0	187	3
Expected 9 : 1		396.0	44.0	20.7	2.3	21.6	2.4	153.0	17.0
Expected, constant selection		349.0	91.0	15.2	7.8	23.4	0.6	154.4	15.6

The approximate numbers of birds involved in each experiment are given at the heads of the columns.

Table 1. (Cont.)

Experiment 2

20 greens : 180 browns

Date	Hours of observation (BST)	Blackbirds		Observed predation				H. sparrows	
		(2+)		Starlings		Dun-		(many)	
		G	B	G	B	G	B	G	B
9.8.66	9.30-15.15	—	—	0	7	0	1	15	42
10.8.66	10.30-17.30	0	5	—	—	—	—	5	155
11.8.66	10.50-16.10	0	14	1	37	—	—	14	183
14.8.66	15.05-18.10	0	13	0	45	0	2	4	136
15.8.66	11.40-14.10	0	13	0	44	—	—	2	60
17.8.66	14.30-18.35	1	11	1	19	—	—	9	74
18.8.66	10.25-17.40	0	24	1	36	1	4	29	111
Grand totals		1	80	3	188	1	7	78	761
Expected 1 : 9		8.1	72.9	19.1	168.9	0.8	7.2	83.9	755.1
Expected, constant selection*		3.7	77.3	4.5	186.5	2.8	5.2	91.4	747.6

* See text.

and that the direction of the selection could change within a few days. These changes did not seem to be caused by alterations in the colour of the background, which remained apparently constant throughout the period of study.

It remains to enquire whether the differences between the two experiments are related to the frequencies of the colours. On the basis of the grand totals we can calculate for each species the expected numbers of prey eaten, assuming that the selection remained constant throughout the period of study. If this were so the cross-product ratio =

$$\frac{\text{No. of green offered} \times \text{No. of brown eaten}}{\text{No. of brown offered} \times \text{No. of green eaten}}$$

should be the same in both experiments. The expected numbers based on this assumption are given in the second row below the grand totals. It can be seen that in fact all four species took a larger number of common forms than expected and a smaller number of rare ones. Thus the birds appeared to select in a frequency-dependent manner. Direct comparison of observed and expected numbers suggests that the effect is highly significant ($(\Sigma \chi)^2/n = 20.19$ $P \ll 0.0001$). This comparison, however, is not legitimate because of heterogeneity within the series. In experiment 2, for example, the house sparrows took the

Table 2. NUMBERS OF BAITS TAKEN DURING INDIVIDUAL VISITS ON AUGUST 2, 1966

Visit	No. of baits taken	
	G	B
1	4	0
2	7	0
3	3	0
4	3	0
5	9	0
6	5	0
7	5	0
8	2	0
9	0	10
10	24	0
11	3	0
12	5	0
13	1	0
14	0	12
Total	71	22

two colours in different proportions on different days ($\chi_{(4)} = 59.15$ $P \ll 0.001$). Even where there is no significant heterogeneity between days, as with the results from the blackbirds, there is strong evidence that the proportions differed from visit to visit.

Table 2 shows the numbers of green and brown baits taken by blackbirds on August 2, 1966. Each visit by an individual bird is recorded separately. The data are not amenable to analysis by chi-squared, but it is clear that they are very significantly heterogeneous. If the birds were taking the baits at random, but encountering them in the proportions of seventy-one greens to twenty-two browns, then the probability of a bird taking twelve browns in succession (as on visit 14) would be less than 1 in 10^7 . When this heterogeneity is taken into account, the frequency-dependent effects cannot be regarded as formally significant. They nevertheless fulfil predictions based on the hypothesis of apostatic selection.

This hypothesis is further strengthened by a second set of experiments in which "new" birds were familiarized with one colour before they were allowed to feed on a population containing both in equal proportions. The experiments were carried out in a garden near Dalkeith, Midlothian. During 6 days in September 1966, approximately 2,000 green baits were scattered on a background of dark brown soil marked out in a rectangular grid of forty one-metre squares. A population of forty greens and forty browns was then presented to the birds on 3 consecutive days. The greens were somewhat more conspicuous to the human eye. After a lapse of 1 month, the familiarization was repeated with brown baits, after which the birds were again exposed to a population containing forty of each colour. During the second experiment dunnocks, house sparrows and robins were feeding at the same time as the blackbirds. It was, however, only practicable to observe the blackbirds. Predation by "small birds" was deduced from an examination of the baits at half hour intervals. The results are given in Table 3.

In each case the blackbirds took more of the familiar colour. The trend is highly significant despite the hetero-

Table 3. DAILY TOTALS OF BAITS TAKEN AFTER FAMILIARIZATION WITH ONE COLOUR ALONE: SOIL BACKGROUND

	Date	Hours of observation (BST)	Observed predation			
			Blackbirds		"Small birds"	
			(8+)		(many)	
			G	B	G	B
Familiarized with greens	6.9.66	14.30-21.00	50 (9)	9 (1)	—	—
	7.9.66	11.15-19.00	111 (13)	14 (0)	—	—
	8.9.66	6.20-18.22	153 (32)	75 (8)	—	—
		Totals	314 (53)	98 (9)	—	—
Familiarized with browns	15.10.66	8.25-16.05	52 (8)	103 (20)	110	254

For an explanation of the numbers in parentheses, see text.

geneity between visits. This point is well made by the figures in parentheses in Table 3, which record the numbers of visits during which the specified colour was taken in excess. For each day these figures depart significantly in the expected direction from a 1 : 1 ratio. After familiarization with greens there was a significant increase in the percentage of browns taken by blackbirds over every five visits ($P < 0.01$, Spearman's rank correlation test), suggesting that the birds were gradually recognizing the browns as acceptable food. During the single day after familiarization with browns there was no corresponding increase in the number of greens taken by blackbirds, but the "small birds" did show such a trend ($P < 0.01$).

The heterogeneity between visits, found in both sets of experiments, suggests that individual birds may differ in their preferences ("specific searching images"¹) for particular colours. This suggestion has been confirmed for greens and browns by observations on colour-ringed blackbirds (Allen, in preparation). The second set of experiments indicates that these preferences can change systematically as a result of frequent encounters with a particular colour. Such behaviour would be expected to give rise to the frequency-dependent effects shown in Table 1.

In summary, ground-feeding passerines, which are important predators of many polymorphic species of insects and molluscs, appear to hunt in a manner that would tend actively to maintain colour polymorphisms in their prey.

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JOHN A. ALLEN
BRYAN CLARKE

Department of Zoology,
University of Edinburgh.

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Evidence for Stabilizing and Apostatic Selection
by Wild Blackbirds

WHEN predators concentrate on rare varieties of prey species, as previous work has suggested¹⁻⁴, there is a tendency towards the elimination of variability. This type of selection is stabilizing⁵. When predators choose the most common varieties, the selection is apostatic⁶ and may result in the maintenance of variability⁶⁻⁹. My results (ref. 10 and in preparation) with wild blackbirds (Turdus merula L.) and artificial prey suggest that selection may be stabilizing or apostatic according to the density of the prey.

The prey were cylindrical (0.7 cm long x 0.7 cm diameter) lard-and-flour baits coloured green or brown⁷. In a first set of experiments, during April and May 1968, closely packed baits were distributed at random in two circular (19 cm diameter) metal sieves. One sieve contained 30 greens and 270 browns, the other 270 greens and 30 browns. They were placed 1 m apart on the lawn at the Department of Zoology, University of Edinburgh. Predation was confined to a pair of blackbirds and the number of baits taken was deduced from a frequent examination of the sieves. Eaten baits were replaced to ensure that the 9:1 ratios were kept constant. The populations were presented daily for 2 to 4 h and their relative positions were frequently altered throughout the 37 days of the study.

Table 1 gives the grand totals of baits taken and the results expected on the basis of no selection. The blackbirds clearly

Table 1. Grand Totals of Baits taken from 9:1 Populations
presented at Maximum Density

Dates of presentation (1968)	Population 1 9 green: 1 brown		Population 2 1 green: 9 brown	
	G	B	G	B
April 22-May 27	1,606 (1,978.2)	592 (219.8)	743 (168.5)	942 (1,516.5)

Population size = 300 baits. Figures in parentheses represent the expectation if the baits were taken in proportion to their frequencies. G, green; B, brown.

tended to select the rarer colours. This result is statistically highly significant.

In a second set of experiments, carried out between 1966 and 1969, populations were presented at densities of two baits per square metre on lawns and grass fields near Edinburgh. Including a preliminary study⁷, eleven experiments gave data for blackbirds alone, and in one case predation by a single songthrush (Turdus philomelos Hart.) is included. The populations usually consisted of 200 baits distributed at random in grids of 100 one-metre squares, each metre square containing two baits. In one experiment 100 baits were randomly distributed in a grid of 50 one-metre squares. The populations of three experiments were observed continuously. Others were sometimes left unattended for short periods, after which they were examined to determine the number of baits removed. In each experiment the spatial distribution of the baits was altered daily and eaten baits were replaced frequently. In five experiments the populations were first presented with greens nine times as common as browns, followed by populations with browns nine times commoner than greens. In the remaining six experiments the populations were presented in the reverse sequence. The experiments varied in length, but most lasted for about 2 weeks.

The overall results are given in Table 2. We must enquire whether selection was related to the frequencies of the colours. If selection had remained constant throughout a given experiment the cross-product ratio:

$$\frac{\text{No. of green offered} \times \text{No. of brown eaten}}{\text{No. of brown offered} \times \text{No. of green eaten}}$$

Table 2. Grand Totals of Baits taken from 9:1 Populations presented at Densities of 2/m²

Expt.	Nos. of blackbirds	9 green : 1 brown → 1 green : 9 brown				$\chi^2_{(1)}$	P
		G	B	G	B		
1 [*]	6 +	354 (348.9)	86 (91.1)	1 (3.7)	80 (77.3)	2.38	NS
5.2	4	353 (343.0)	56 (66.0)	11 (17.4)	278 (271.6)	4.32	<0.01
5.3	2	231 (217.0)	40 (54.0)	7 (14.5)	299 (291.5)	8.60	<0.01
5.4	2	192 (175.6)	39 (55.4)	6 (13.6)	348 (340.4)	10.82	<0.01
6.2	4	619 (601.3)	148 (165.7)	5 (13.6)	315 (304.4)	8.13	<0.01

Expt.	Nos. of blackbirds	1 green : 9 brown → 9 green : 1 brown				$\chi^2_{(1)}$	P
		G	B	G	B		
2.1 [*]	2 and 1 songthrush	1 (1.1)	312 (311.9)	92 (91.5)	327 (327.5)	0.01	NS
4 ^{**+}	2 +	0 (3.3)	232 (228.7)	117 (103.1)	74 (87.9)	7.46	<0.05
3.3 [†]	10 +	2 (4.0)	734 (732.0)	63 (50.5)	102 (114.5)	5.44	<0.02
5.1	4	3 (13.5)	368 (357.5)	372 (348.0)	90 (114.0)	15.18	<0.001
5.5	5	3 (14.2)	350 (338.8)	380 (356.1)	81 (104.9)	10.25	<0.001
6.1	4	4 (16.5)	606 (593.6)	411 (375.4)	131 (166.6)	20.72	<0.001

Populations size = 200 baits except where shown. Figures in parentheses represent the expectation assuming constant selection.

G, green; B, brown; NS, not significant.

* Continuously observed.

+ The two "9:1" populations were separated by a period of presentation of "1:1" populations.

† Population size = 100 baits.

should be the same during both parts of the experiment. The expected grand totals based on this assumption are given in Table 2. In nine cases the deviations from expected were statistically significant, but such direct comparisons of observed and expected numbers are not strictly legitimate, because of heterogeneity within the experiments^{7, 10}. In all eleven experiments the blackbirds took a larger number of common forms than expected and a smaller number of rare ones. This proportion of "successes" is statistically significant ($P < 0.001$, binomial test). The results therefore appear to be consistent, despite heterogeneity.

To summarize, selection by wild blackbirds seems to be stabilizing when baits are at a very high density and apostatic when the density is lower. Predation would presumably be random at some intermediate density. At very high prey densities predators may tend to form "specific searching images" for uncommon varieties, because they stand out against a background of the common sorts^{2,4} or because they are odd^{1, 3}. When prey are at low densities predators will have to search more actively and may profit by the formation of specific searching images for common varieties⁶. Predation may be random at very low prey densities¹¹. What constitutes "very high", "low", or "very low" densities of prey in a given environment will depend on the particular species of predator and prey.

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JOHN A. ALLEN

Department of Zoology, PO Box 35064,
University of Dar es Salaam,
Dar es Salaam, Tanzania

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