PROTECTIVE COLORATION AND FREQUENCY-DEPENDENT SELECTION: RESPONSES OF BIRDS TO PREY COLOUR PATTERNS

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To Glenn and to my Parents

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ABSTRACT

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PROTECTIVE COLORATION AND FREQUENCY-DEPENDENT SELECTION: RESPONSES OF BIRDS TO PREY COLOUR PATTERNS

by Deborah Lyn Raymond

Animal coloration in defence against predators has been discussed for over a hundred years. Early works were mainly descriptive and often assumed that any difficulties experienced by humans in detecting animals were also experienced by visual predators. Subsequent evidence for cryptic coloration was surmised from convergent evolution of colours and patterns and from correlations between backgrounds and particular colours and patterns. There is strong circumstantial evidence but relatively little experimental evidence that the colours and patterns of animals actually afford protection against visually hunting predators. Many prey species that are polymorphic for coloration also appear to be cryptic, and it has been suggested that predators may select colour patterns in a frequency-dependent manner and thereby maintain such colour pattern polymorphisms. The experiments described in this thesis used striped colour patterns to investigate protective coloration and frequency-dependent selection.

Birds were offered choices between prey differing in their colour patterns. The ultimate effects on the prey selection were studied. Artificial prey made from coloured pastry were used for all experiments except one in which pastry-filled *Cepaea hortensis* shells were used. The pastry prey were flat and striped coloured patterns could be applied. Predators were wild birds in all but one of the experiments, where domestic chicks were used. Three basic experimental designs were involved: simple choice tests to investigate colour patterns and crypsis; training experiments where birds were trained on one prey type and then given a choice between two or more prey types; experiments with populations of two prey types at different densities and frequencies to test for frequency-dependent selection.

The first experiment used flat artificial backgrounds and results indicated that striped prey were at a slight advantage on a matching striped background. Subsequent experiments were carried out on grass, which presented a more complex and three-dimensional background. Choice tests showed that prey with a ground colour that matched the grass were at an advantage over unmatching prey and that a matching stripe gave an added advantage. Observations showed that some birds avoided white prey types with a red stripe but not green prey types with a red stripe. Experiments were undertaken with plain and striped brightly coloured prey types. Birds tended to avoid the plain brightly coloured prey types and the possible reasons for this are discussed. Training experiments showed that wild birds can become trained to search for a prey type on the basis of the presence or absence of a coloured stripe or on banded and unbanded *Cepaea hortensis* shells. The effect of training decreased when the prey types became more similar and when the training period was shorter. Overpredation of the familiar prey type could result in apostatic selection and the maintenance of polymorphism in prey species in which the morphs are distinguished by colour patterns. Further experiments with prey types that differed only very slightly in their colour patterns found that, in one series where the training prey type was the same throughout, as the birds became more familiar with one prey type they took proportionally more of the unfamiliar prey type, suggesting that training effects or overpredation of common prey found in experiments may only be short-term. Chicks, which were trained on one prey type and then given a choice between prey types that did not include the training prey type, preferred the prey type that was most similar to the training prey type. Experiments involving a range of prey densities and frequencies found anti-apostatic selection at the prey density of $30/m^2$, both apostatic and anti-apostatic selection at the prey density of $3850/m^2$ ('maximum') and no frequency-dependent selection at two lower prey densities. The experiments reported in this thesis show that birds can discriminate between very similar colour patterns, that they can select on the basis of colour patterns and that this selection can be frequency-dependent.

CHAPTER 1 INTRODUCTION

Who can paint
Like Nature? Can imagination boast,
Amid its gay creation, hues like hers?
James Thomson (1726-30)
"Spring"
The Seasons

Nature is one with rapine, a harm no preacher can heal;
The Mayfly is torn by the swallow, the sparrow speared by the shrike,
And the whole little wood where I sit is a world of plunder and prey.
Alfred Lord Tennyson (1856)
"Maud, A Monodrama"

1.1 COLORATION IN GENERAL

Colour is the sensation that results from the reception of visible radiation by the eye, and is defined by the wavelength of the radiation. White light is a combination of many electromagnetic wavelengths that range from just below 400 nm at the violet end of the spectrum to about 750 nm at the red end. The other colours are produced by rays that fall between this range. Wavelengths shorter than about 400 nm are in the ultraviolet and can be seen by some fishes, insects and birds. Wavelengths longer than 750 nm are in the infrared. A good introduction to this subject is provided by Chamberlin and Chamberlin (1980).

Colour vision is particularly well developed in reptiles and birds, and fish also have colour vision. Many mammals are thought to have little or no colour vision, while others have very limited colour vision and that of others is less restricted. It is largely agreed that the eye of the insect is not sensitive to the red region of the spectrum.

When white light falls on an object, some or all of its components may be reflected. Those components that are not reflected are absorbed and the colour of the object that we see is due to the reflected rays. Colours produced by the removal of some of the components of the incident light by the physical structure of the object's surface are known as structural colours. Colours that are the result of the chemical nature of the surface absorbing some of the wavelengths are known as pigmentary colours.

The colours of animals may be due to both structural and pigmentary colours. Examples of structural colours include the mother-of-pearl found in mollusc shells, the iridescence of a male peacock's tail feathers, the blueness of the feathers of many birds such as the budgerigar and blue tit, iridescent colours in many insects, and the whiteness of Lepidoptera, fur and feathers. The structural colours of animals may be due to the scattering of light, to interference or to diffraction.

Pigmentary colours give browns, greens, yellows and reds and are produced by many different chemicals. For example, melanins are responsible for many of the dark colours of animals, especially the blacks and browns. Colour can also be produced by the tanning of proteins: an example is sclerotin, found in insect cuticles, which is a hard brown tanned protein. The carotenoids are carbon based pigments that are responsible for many of the reds, oranges and yellows found in many animals, and, when linked with a protein, may also produce such colours as blue and violet. Together with melanins, carotenoids are probable the most widespread of all animal pigments and they occur in all the phyla. Other chemical pigments are the porphin derivatives, the bilin derivatives, quinones, guanine, pteridines, flavins and omnochromes. (For a review see Fox and Vivers, 1960.)

Colour has been classified in terms of three dimensions: hue, value and chroma (eg. Munsell, 1967). Pure spectral hues are produced when sunlight is refracted by a prism. Any hue can be modified by determining its degree of lightness or darkness according to the amount of light reflected from a surface or radiated from a source. The usual term for this dimension is 'value'. Pure hues in any surface colour can be modified by the addition of blackness or whiteness in such a way that the differences in value are constant and continuous to form a two-dimensional monochromatic scale of value. The third dimension of the classification of colour is 'chroma'. Chroma relates to the ratio of pure hue to greyness in the appearance of a colour: the more saturated it is the stronger it appears.

A 'pattern' can be defined as a mosaic of spots, stripes or patches of various sizes and shapes, and the colours and pattern on the surface of an animal together constitute its 'colour pattern' or its 'coloration'. This thesis is concerned with the evolutionary adaptations of animal coloration, and in particular the functions of colour pattern in providing protection from predation.

1.2 PROTECTIVE COLORATION

Ultimately, the external colour of an animal's body results from the interaction between the evolutionary forces that are significant to that animal's survival. There are three main selective forces affecting animal colour and pattern: (1) heat exchange and radiation; (2) intraspecific or interspecific communication; (3) predation. (Hamilton, 1973). Other kinds of coloration may be incidental, revealing underlying physical or physiological conditions.

As already mentioned, the third agent, predation, is the selective force that this thesis is concerned with. Its effect has been called 'protective coloration', a term that not only describes coloration which protects prey from potential predators but also coloration that hides predators from their prey. The colours and patterns of an animal are usually used for primary defence against predation (defences that decrease the probability of detection or recognition by a predator and that operate regardless of whether or not there is a predator in the vicinity, *cf.* Edmunds, 1974). Coloration can also act in secondary defence against predation to increase the chances of a prey's survival during an actual encounter with a predator.

1.2.1 Primary Defences

Primary defensive mechanisms that use protective coloration are crypsis, mimicry and aposematism (Edmunds, 1974).

a) Crypsis

In crypsis the predator fails to detect the prey object. Crypsis will be discussed in the next section (Section 1.3).

b) Mimicry

If the predator detects the prey but fails to recognise it as something edible this defence can be defined as 'mimicry'. Mimicry is the resemblance of one animal (the mimic) to another object or organism (the model) with the result that a second animal is deceived into confusing the two. The problem of whether mimics that resemble objects such as sticks are cryptic or mimetic is discussed in Section 1.3.2.

(c) Aposematic Coloration

Coloration can also be used by unpalatable or potentially dangerous animals to signal a warning to predators, and thereby hope to avoid attack. This type of coloration is called 'aposematism' and consists of bright colours and contrasting patterns. The avoidance of aposematic animals by predators is the result of either a learned response or an innate response. For it to be a learned response the predator must have sampled the aposematic prey type and then been capable of associating the coloration with unpalatability or danger. It is possible that many of these prey animals are cryptic from a distance but conspicuous, and thus aposematic, at close quarters (Edmunds, 1974).

1.2.2 Secondary Defence

Colours and patterns can also be used in secondary defence, which operates during an encounter with a predator. 'Flash coloration', 'startle displays' and 'deflective coloration' are three instances where coloration can be used in attempting to escape from a predator.

'Flash coloration' is a way of deflecting a predatory attack. If a prey animal is discovered, it may flee for a short distance and then rest motionless and cryptic. It may exhibit flash coloration by showing a flash of colour as it moves, which then disappears when it comes to rest. The theory is that the predator may follow the colour, becomes confused by its sudden disappearance and then may lose the prey animal altogether.

'Startle displays' occur when an animal responds to its discovery by a predator by adopting a characteristic behaviour that appears to be designed to intimidate the predator. Coppinger (1969, 1970) and Blest (1957) have shown that some birds exhibit escape behaviour when they are confronted by the sudden appearance of bright colours. Many moths, for example, which are cryptic at rest during the day, resort to startle displays when they are suddenly disturbed or attacked. Such displays usually involve the exposure of bright colours on the hindwings, and the displays deter a predator from attacking or, if the display occurs when the moth is caught, cause the moth to be released (Sargent, 1976, 1978). Circular patterns have also evolved for use in startle displays. Blest (1957) showed that the closer in appearance such 'eyespots' were to a vertebrate eye the greater the escape response that was elicited from a number of birds. These results were confimed in a series of experiments on starlings, *Sturnus vulgaris* (Inglis, Huson, Marshall and Neville, 1983).

'Deflective coloration' is a means of deflecting a predator's attention onto some area of the prey's body where an attack is less likely to be fatal. Deflection marks may direct an attack in this way. For example, small eyespots on the wings of various butterflies may act to concentrate the attention of the predator in that area and away from the insect's head and body (Cott, 1940; Blest, 1957).

This thesis is concerned with prey coloration and its effects on detection by predators and prey selection, and therefore the use of protective coloration as a secondary defence is excluded.

TABLE 1.1: Crypsis - Summary of the means of recognition by sight of a prey object and the corresponding steps toward protection from predators.

MEANS OF RECOGNITION	METHOD OF PROTECTION
Prey appears as a continuous area differing in hue, purity and depth from its surroundings.	Colour and pattern resemblance between the prey and background.
Due to unequal illumination on an uneven surface, prey will be thrown into relief by effect of light and shade, allowing surface contours and details to be detected.	Countershading, which eliminates the shadowed areas of the prey by colouring the surface nearest the light darkest.
The prey is framed by an outline, and this outline frequently has a characteristic or familiar shape enabling it to be recognised.	Disruptive coloration, where a superimposed pattern of contrasted colours and tones serves to blur the outline and break up the real surface form, thus rendering the prey unrecognisable.
A shadow may be thrown by the prey on to its background.	Shadow elimination by modification of form or adaptive orientation.

1.3 CRYPSIS

1.3.1 Crypsis

When a potential prey object is recognised by sight, the means by which the eye distinguishes it are fourfold, and it follows that there are four corresponding steps towards protection from predators (Cott, 1940). These are summarised in Table 1.1. Intuitively, these principles of camouflage appear to be reasonable, but surprisingly little work has been done to verify them.

For an animal to be 'cryptic' its colour pattern must resemble a "random sample of its background as perceived by its predators at the time, at the age and in the microhabitat where the prey is most vulnerable to visually hunting predators" (Endler, 1978). Edmunds (1974) has also restricted the term 'cryptic' to describe those animals that "are not normally distinguished from the environment" and therefore are overlooked by a predator.

The visibility of an animal to a potential predator is affected not only by the inherent properties of the animal's colour pattern but also by the predator's vision and hunting tactics. For example, it has long been thought that certain patterns only become cryptic after they are blended with distance (Poulton, 1890; Mottram, 1915, 1916). Mottram (1915) gave examples of animal colour patterns that appear to show obliterative shading as a result of pattern blending such as the black and white stripes of different species of zebra (*Equus sp.*), which appear to blend at comparatively short distances, especially at twilight. A main predator of the zebra is the lion, which is short-sighted when compared with humans and may not see zebra until they are within close range. Similarly, Pietrowicz and Kamil (1977) have shown that that in blue jays (*Cyanocitta cristata*) the difficulty of recognising moths cryptic on trees increases with distance and therefore blue jays should forage close to the backgrounds on which their potential prey rest. In addition, the prey's own behaviour will also affect its visibility. Movement, for example, is often important: prey should be static in a static background but should move in unison with a moving background.

If the colour pattern is to be cryptic then the patches of a colour pattern should represent those of the background. Grain, colour diversity and contrast are the aspects of the pattern that should be matched as closely as possible. This theme is stated in the works of Thayer (1909), Mottram (1916), Cott (1940), Wickler (1968), von Frisch (1973) and Edmunds (1974), and is implicit in the concepts they developed: for example, disruptive coloration, differential blending, countershading and general resemblance. Examples of matching with respect to grain are the wing patterns of moths and the bark on which they rest (Sargent and Kleiper, 1969). The colour reflectance curves of the middorsal surfaces of amphibians and reptiles living in California, U.S.A., and the colour reflectance curves obtained from samples of the backgrounds on which the animals were captured are very similar (Norris and Lowe, 1964); the colour patterns of the animals appear to be composed of a mixture of patches similar to the background colours. In a study of the convergences of colour patterns among several coexisting mimicry complexes of neotropical butterflies, Papageorgis (1975) found that each complex flies within a different height range, and therefore bird predators see each complex against different background colour patterns. The change in the colour composition of the background from the forest floor up to the canopy is paralleled by a change in the colour compositions of the patterns of each mimicry complex. This suggests that these patterns may be cryptic against the background of the forest interior.

The general brightness of an animal's body compared with the background has been examined in a number of species (for example, in moths: Kettlewell, 1973; and in pelagic animals: Hemmings, 1966, 1974) but this does not give information about any contrast within its colour pattern.

There are also many instances of shape resemblance of colour patterns and backgrounds. Arthropods, frogs, birds and fish living in grasses or reeds often possess vertical stripes as part of their colour pattern (Cott, 1940; Wickler, 1968; Fraser Rowell, 1971; Stewart, 1974). The resting behaviour (for example, orientation of the animal's striped colour pattern with regard to its background) is often important for these animals.

Many species that appear to be cryptic possess colour patterns which consist of stripes or have a single dominant stripe. This is true of colour patterns found on animals in almost all phyla. Some stripes are thought to act in a disruptive way. For example, a conspicuous stripe along the middle of an animal's back, as seen in many frogs, toads, caterpillars and grasshoppers, may break up the shape of the animal into two parts. This disrupts the bilateral symmetry, and each half may be less recognisable to a predator than the animal as a whole (Cott, 1940). It is possible that the striped pattern also represents a sample of the animal's background.

There are many ecological studies on animals that possess striped colour patterns. Detailed studies of vertebral stripes have been made in north temperate *Acris* (Pyburn 1961a,b; Isaacs, 1971; Milstead, 1971; Gray, 1972), *Pseudacris* (Matthews, 1971) and *Rana sylvatica* (Browder, Underhill and Merrell, 1966; Fishbeck and Underhill, 1971), neotropical *Eleutherodactylus* (Goin, 1954; Savage and Emerson, 1970) and *Plethodon cinereus* (Williams, Highton and Cooper, 1968). Many striped patterns can be seen in tree frogs (Schiøtz, 1967); and examples from Malawi of grass-dwelling tree frogs that have striped patterns are given by Stewart (1974), of which at least twenty-two species have vertebral stripes. Many snakes have striped colour patterns (Camin and Ehrlich, 1958; Gregory, Gregory and Macartney, 1983). Striped patterns in invertebrate species are numerous: examples occur in Mollusca (Holmes, 1940; Owen, 1963; Smith, 1975; Jones, Leith and Rawlings, 1977; Heller, 1981; Heller and Volokita, 1981a,b; Allen, 1983; Berry, 1983; Reid, 1987), Isopoda (Bocquet, 1953; West, 1964), Arachnida (Oxford, 1983) and Insecta (Owen, 1963; Fraser Rowell, 1971; Mariath, 1982; Westerman and Ritchie, 1984; Rotheray, 1986). According to Weismann (1904), the colour patterns of sphingid caterpillars fall into three categories, each of adaptive significance to animals in particular habitats. Caterpillars with longitudinal stripes live on plants among grass or in grass itself; their general body colour corresponds to their background, but larger animals exhibit white, longitudinal lines. Caterpillars with transverse stripes live on trees and bushes; and Weismann suggests that their colour pattern imitates the lateral veining of leaves. There are also some caterpillars which display spots of various sizes. Weismann suggests that these spots have a variety of functions such as warning colours or flash coloration and possibly mimicry of berries in the background. However, most of the studies listed above give little information about the functions of the striped colour patterns and do not positively identify them as cryptic.

1.3.2 The Difference Between Crypsis, Masquerade and Batesian Mimicry

There has been much debate on whether the resemblance of an animal to an inedible object such as a leaf or bird-dropping should come under the heading of 'crypsis', 'Batesian mimicry' or 'masquerade' (Vane-Wright, 1980; Edmunds, 1981; Endler, 1981; Robinson, 1981; Allen and Cooper, 1985). Much of this discussion has been generated by the lack of knowledge of how the brain of a predator receives the signals generated by the prey and its background in the different circumstances. Batesian mimicry is usually restricted to describe an edible prey species mimicking an inedible object living in the same area (eg. Cott, 1940; Edmunds, 1974), but Endler (1981) separates Batesian mimicry and masquerade, and he shows the distinction between Batesian mimicry, masquerade and crypsis. In crypsis, the mistake in discrimination by the predator depends on the relationship between the prey and its background; in Batesian mimicry, it depends on the similarity to a specific species (for example, Diptera mimicking bees and wasps); and in masquerade, it depends on the similarity to a specific object (examples are stick-mimics, leaf-mimics and insects that resemble bird droppings). Batesian mimicry and masquerade are further distinguished on the grounds that, in masquerade, any attack by the predator on the mimic will have no effect on the model's population dynamics; whereas, in Batesian mimicry, the mimic's and the model's population dynamics are linked. In this thesis, the term 'crypsis', as defined by Endler (1978), will be used to mean that an animal's colour pattern resembles a random sample of its background as perceived by its predators and the term 'masquerade' will be used to describe the situation where an animal mimics a specific object in its environment.

1.4 EVIDENCE FOR VISUAL SELECTION ON CRYPTIC COLOUR PATTERNS

Early works on the protective functions of animal colour patterns were mainly descriptive (eg., Poulton, 1890). The evidence for cryptic colour patterns was subjective and often assumed that any difficulties experienced by humans in detecting animals were also experienced by visual predators of those animals. Of course, the vision of most animals is very different from that of humans; birds, for example, have eyes that are more sensitive to ultra-violet light (Bowmaker, 1980) and, unlike primates, pigeons possess good visual acuity across the entire retinal area and can detect objects without having to achieve the precise fixation that we require (Blough, 1979). In later works, much evidence for cryptic coloration was surmised from convergent evolution of colours and patterns (egs., 'common cryptic coloration', Cott, 1940; recently Atkinson and Warwick, 1981 on *Littorina rudis* and *L. arcana*; Endler, 1982 on *Poecilia reticulata* and *Phalloceros caudimaculatus*; Goodfriend, 1983 on *Eutrochatella pulchella* and *Viana regina*) and from correlations between backgrounds and particular colours and patterns (egs., Cain and Sheppard, 1950, Arnold, 1970 and Greenwood, 1974 on *Cepaea nemoralis*; Giesel, 1970 on *Acmaea digitalis*; Savage and Emerson, 1970 on *Eleutherodactylus bramsfordii*; Parkin, 1973 on *Arianta arbustorum*; Gill, 1979 on *Chorthippus brunneus*; Reimechen, 1979 on *Littorina mariae*; Heller, 1981 on *Theba pisaria*; Heller and Volokita, 1981a,b on *Xeropicta vestalis*; Cook, 1983 on *Littorina sp.*; Rotheray, 1986 on aphidophagous syrphid larvae). These are examples of very strong circumstantial evidence but there is relatively little experimental evidence that the colours and patterns described actually afford protection from visually hunting predators.

Sampling of predated individuals and comparing the proportions of different colour patterns with those found in the natural populations have resulted in more direct evidence for visual selection on colour (for example: Sheppard, 1951; Bantock, Bayley and Harvey, 1974) and pattern (for example: Truman, 1916; Cain and Sheppard, 1954; Arnold, 1966; Carter, 1968; Bantock, 1971; Smith, 1975). 'Mark-release-recapture' techniques have been used in many studies on industrial melanism in Lepidoptera, the most well-known of which are those of Kettlewell (eg., 1955, 1956, 1973).

Cepaea nemoralis (and its close relative *C. hortensis*) has been intensively researched for over sixty years (reviewed by Murray, 1975 and Jones *et al.*, 1977; Clarke *et al.*, 1978; Cain, 1983). This species of snail is polymorphic (see next section 1.5) for its shell colour and for the presence and number of up to five dark brown bands running along the whorls. The shell colour may be classed as either yellow, pink or brown, and the commonest banding patterns are unbanded (00000), 5-banded (12345) and mid-banded (00300). There is also variation within the banding patterns, such as fusions of adjacent bands or loss of band pigments. *C. nemoralis* is also polymorphic for the colour of the lip of the shell and for body colour. The genetics of this polymorphism are well known. The order of dominance for shell colour is brown, pink, yellow; and unbanded is dominant over banded. The genes controlling shell colour, banding pattern, lip colour and type of band pigmentation are linked together as part of a supergene.

C. nemoralis is found in western Europe in a wide range of habitats. There have been regional and local studies made throughout Europe (see Cain, 1983). There is great variation in the morph frequency of *C. nemoralis* in different areas, sometimes even between areas only a few hundred metres apart.

One of the selective forces that may act on the colour polymorphism in *C. nemoralis* is that of predation by animals which hunt by sight. Correlations have been found between morph frequency and types of habitat in the Oxford area (Cain and Sheppard, 1954). Cain and Sheppard (1954) argued that this correlation was due to the most cryptic morph being favoured in any particular habitat. Yellow banded snails were most commonly found in 'grassland' and brown unbanded snails most commonly in 'beechwoods'.

Variation in *C. nemoralis* in relation to the temporal stability of the habitats was studied by Cameron and Dillon (1984) and Cameron and Pannett (1985). In areas of more stable habitats there was pronounced variation with habitat of the colour pattern, and correlations suggested visual selection for crypsis and supported the findings of Cain and Sheppard (1954). In more unstable habitats, such as the downlands, there was no variation with habitat and it has been suggested that any variation is due to the histories of the snail populations (Cameron, Carter and Palles-Clark, 1980). The variation with habitat at the colour locus was greater than at the loci for banding (Cameron and Pannett, 1985) and most of the evidence for selection for crypsis has been for the shell colour polymorphism. There is less evidence for the visual selection on the banding polymorphism (Clarke *et al.*, 1978; Cameron and Pannett, 1985).

The song thrush (*Turdus philomelos* Brehm.) is a known predator of snails. Various studies have been made comparing morph frequencies in snail populations with those found on nearby thrush anvils (for example: Lamotte, 1950; Sheppard, 1951; Cain and Sheppard, 1954; Murray, 1962; Wolda, 1963; Arnold, 1966; Carter, 1968).

Sheppard (1951) studied two isolated *C. nemoralis* populations in clearings in woodland near Oxford. He collected shells destroyed by song thrushes and calculated the proportions of the morphs in the samples and compared them with those in the living populations. He found that there was a decrease in the proportion of yellow snails taken during the year from April to June. He attributed this to the yellow morphs becoming better protected in their habitats, which were becoming greener and yellower with the increasing foliage. Wolda (1963) found similar changes in the proportions of yellow morphs in the thrush-predated samples during the spring. However, Wolda found that in May there was an increase in the frequency of yellow morphs in the thrush-predated samples and he could not correlate this to any changes in background colour. Carter (1968), using one of Sheppard's (1951) sites, found that yellow morphs were at a disadvantage during the summer months, which he attributes to dense and tall herbage giving rise to a dark background near the ground. He also found that the two pre-experimental snail populations of his in 1963 and Sheppard's in 1951 had very similar frequencies of the yellow morph even though Sheppard had introduced an experimental population, which had altered the morph frequencies considerably. Therefore, there appeared to be selection for a particular frequency of yellow in the population and predation seemed to be one of the agents of selection.

If visual selection acts in favour of the most cryptic morph in any given habitat, then monomorphism would be the expected outcome; (see, however, Jones *et al.*, 1977 for discussion of other selective forces such as climatic selection). Whether apostatic selection (Section 1.6.3) by birds or other predators feeding on polymorphic snails such as *C. nemoralis* and *C. hortensis* could be a factor in the maintenance of the polymorphisms has been discussed by many authors; (for reviews see Jones *et al.*, 1977; Clarke *et al.*, 1978; Cain, 1983). Harvey, Birley and Blackstock (1975) presented wild song thrushes with populations of *Cepaea* shells filled with bread and found that experience influenced the birds' choices of shell colour: they preferred the familiar colour. It is arguable that such behaviour could result in apostatic selection maintaining a shell colour polymorphism.

Some experiments in which predation has been actually observed have been performed to study visual selection on cryptic coloration, usually by giving predators a choice between prey that did or did not match their backgrounds. The majority of these experiments have used prey that differed only in their general coloration and not in their colour patterns (Di Cesnola, 1904; Young, 1916; Eisentraut, 1927; Sumner, 1934; Carrick, 1936; Isely, 1938; Popham, 1941, 1943a,b; Dice, 1947; Ergene, 1951, 1953; Bantock and Harvey, 1974; Czaplicki and Porter, 1974; Wicklund, 1975; Pietrewicz and Kamil, 1977; Tordoff, 1980; Kerfoot, 1980; Mariath, 1982). Comparatively few experiments have been performed that have concentrated on prey colour **patterns** (other than studies on warning coloration and mimicry of distasteful species). Turner (1961) used artificial prey with different ground colours and presented them on a lawn background to wild birds. He found that the addition of a fawn stripe to his green prey resulted in this striped prey type being eaten significantly less than green or fawn prey without a stripe. He attributed this result to the stripe acting disruptively and rendering the prey type more cryptic. Natural selection on the colour patterns of guppies (*Poecilia reticulata*) have been studied by Endler (1978, 1980, 1982). The colour patterns of guppies are highly variable and consist of a mosaic of spots or patches that vary in colour, size, position and reflectivity. Endler (1980) examined the effects of predation intensity and patch size on the colour patterns of guppy poulations and found that background matching was good: for example, populations living on coarse gravel had larger spots than populations living on fine gravel, within a given predation intensity. This effect disappeared in the absence of predation and resulted in sexual selection in favour of conspicuous colour patterns. The hypothesis that the colour patterns of guppy populations are the result of a balance between sexual selection and defence from predation was supported. Further studies on the functions of colour patterns in inconspicuous prey have been needed needed and the first part of this thesis reports experiments of this type.

1.5 COLOUR PATTERN POLYMORPHISM

Many cryptic prey species have non-mimetic colour pattern polymorphisms and one field of study in which visual selection by predators has been of great interest is in the maintenance of these colour pattern polymorphisms as balanced polymorphisms. A 'polymorphism', as defined by Ford (1940), is the occurrence together in the same area at the same time of two or more discontinuous forms of a species that are not maintained by mutation alone.

Poulton, in 1884, first argued that a larval dimorphism might be of advantage if the colours of the two morphs were protective. The range of backgrounds on which that species would be concealed would be widened and predators might take more time searching for a dimorphic species (Poulton, 1890). Poulton (1884) also set out the basis for an argument for frequency-dependent selection by predators maintaining a balanced polymorphism in non-mimetic prey (see Allen and Clarke, 1984). If predators overeat the commonest morph, selection will then favour rare morphs and this could result in the maintenance of the polymorphism. Clarke (1962) coined the term 'apostatic selection' for this type of frequency-dependent selection (the reverse is 'anti-apostatic' selection where predators disproportionately overeat the rarest morphs, Greenwood, 1984).

Although the theory has been discussed for many years (Poulton, 1884, 1890; Cain and Sheppard, 1954; Clarke, 1962) that apostatic selection is an important mechanism in the maintenance of colour pattern polymorphisms, evidence was surmised solely from observations of polymorphic populations. The first experiments designed to investigate apostatic selection in wild predators were performed by Allen and Clarke (1968) using conspicuous prey. They presented birds with populations of pastry prey, coloured green or brown in the proportions 1 green:9 brown or 9 green:1 brown, and found that the birds took disproportionately more of the common prey colour. They also performed a series of experiments in which birds were familiarised with one prey colour and then presented with a population of the two prey colours in equal proportions. The birds took more of the familiar prey colour. Further experiments using wild birds and pastry prey have been instrumental in establishing evidence for apostatic selection and for stimulating discussion (Allen, 1972, 1973, 1974, 1976, 1984; Manly, Miller and Cook, 1972; Cook and Miller, 1977; Fullick and Greenwood, 1979; Cooper, 1984b).

Frequency-dependent prey selection has also been shown to be dependent on the prey density, although the relationship is unclear (Allen, 1972; Harvey, Jordan and Allen, 1974; Cook and Miller, 1977; Horsley, Lynch, Greenwood, Hardman and Mosely, 1979; Willis, McEwan, Greenwood and Elton, 1980; Allen and Anderson, 1984).

The experiments that have been carried out so far have used prey types that differ in colour alone. Many polymorphic species exhibit polymorphisms of colour patterns such as bands, blotches, dots and stripes (Ford, 1964; Endler, 1978). Frequently the polymorphism consists of striped and unstriped morphs. The red-backed salamander *Plethodon cinereus* (Green) has two morphs: a dark unicoloured unstriped morph and a morph with a prominent red dorsal stripe (Williams, Highton and Cooper, 1968). *Natrix sipedon* L., a species of water snake, is polymorphic for banding patterns (Camin and Ehrlich, 1958). The garter snake *Thamnophis melanogaster canescens* has various colour pattern groups, which include lateral stripes, dorsal stripe, ventral stripe and dorsal blotches, and is polymorphic for the presence or absence of these pattern groups as well as having a morph that possesses none of them (Gregory, Gregory and Macartney, 1983). Dorsal stripe polymorphisms are found in many anuran species (Goin, 1954; Browder, Underhill and Merrell, 1966; Schiøtz, 1967; Fishbeck and Underhill, 1971; Gray, 1972; Stewart, 1974). Many species of grasshopper are polymorphic for longitudinal striped patterns: examples can be found in the review of Acridoid grasshopper coloration by Fraser Rowell (1971). Examples of polymorphism for striped colour patterns can also be found in Mollusca (Owen, 1963; Smith, 1975; Jones, Leith and Rawlings, 1977; Clarke, Arthur, Horsley and Parkin, 1978; Heller, 1981; Heller and Voloklta, 1981a,b; Cook, 1983; Allen, 1983, 1985; Atkinson and Warwick, 1983) and in Isopoda (Bocquet, 1953; West, 1964). Polymorphism for colour pattern is also found in plant seeds. Dove weed (*Eremocarpus setigerus*) seeds are polymorphic for seed coat pattern (Cook, Atsatt and Simon, 1971; Cook, 1972). There are five seed coat background colours (white, cream, brown, grey or black) and three seed patterns (mottled, striped or uniform black). Unfortunately, little information about the possible camouflage functions of these striped colour patterns is given in these studies.

1.6 PREDATOR BEHAVIOUR IN RELATION TO PROTECTIVE COLORATION

In the 'arms race' between prey and predators, anti-predator adaptations will co-evolve with predator hunting strategies and therefore it is relevant to discuss predator behaviour in more detail.

A common assumption is that predators will forage in an optimal way, and this will be the result of an interaction between the costs and benefits of different foraging strategies (for a review, see Krebs, 1978). Thus a predator should maximise its net rate of food intake (in most instances) while foraging and this will involve 'decisions' with regard to food types, hunting areas and search paths.

1.6.1 Search Behaviour

Food is usually patchy in distribution (Curio, 1976; Krebs, 1978) and therefore the areas in which a predator looks for prey and the path it takes whilst searching the area will determine its chances of encountering its prey. Tinbergen, Impekoven and Franck (1967) suggested that individuals of a cryptic prey species should live at a low density if predators, after discovering one prey item, stay in one area and search in an 'area-restricted' fashion. The results of Tinbergen *et al.* (1967), Croze (1970), Smith (1974a,b) and others confirm that some bird predators will search the area of ground surrounding a prey capture more intensely than before prey capture.

In his studies of the foraging behaviour of blackbirds searching a meadow for either earthworms or artificial prey, Smith (1974b) found that the densities and distributions of the prey populations affected the search paths and speed of movement of the birds. After capturing an earthworm the birds changed their search paths so that for a time they concentrated their search on the area around the capture point. The earthworms were aggregated in the meadow and therefore this change in search behaviour would have been adaptive. Smith also presented the birds with artificial prey populations at two densities ($0.06/m^2$ and $0.299/m^2$) with three different arrangements each. The blackbirds changed the area in which they searched at the higher density so that they remained within the smaller area of the higher density population. At the lower density, with randomly-distributed prey and with clumped prey, the birds modified their search paths and speed of movement after prey capture in a similar way to that following earthworm capture. When the prey distribution was regular, the blackbirds showed no change in their search paths but reduced their overall movement speed. Changes of search paths and speed of movement after prey capture were only found at the lower prey density. It has been suggested by Curio (1976) that this was adaptive if search time was unimportant at high densities; presumably, prey capture at high densities would occur without any modification of search path or speed of movement since the next prey item might be found very quickly after initial prey capture.

The 'area-concentrated' search patterns of some predators, discussed above, may thus affect the distributions and densities of their prey populations.

1.6.2 Choice of Prey

The behaviour of the predator with regard to choice of prey may also have a selective effect on prey populations. It has been suggested that predators should choose the most 'profitable' prey type (Krebs, 1978), this 'profitability' being measured in terms of time taken to find, capture and eat the prey item and the energy value of the food. Prey availability therefore will affect the choice a predator might make as to which prey type it will hunt for. It might benefit a predator to disregard certain prey types altogether if more profitable prey types are in abundance. It might also benefit a predator to choose prey that were easier to find because of their relative conspicuousness.

1.6.3 Behaviour Leading to Frequency-Dependent Selection

There are many ways in which predators may impose frequency-dependent selection on their prey and these are summarised in Greenwood (1984). The relative densities and frequencies of the various prey types within the foraging area of a predator may affect the searching behaviour of that predator. One result could be that the predator will show a frequency-dependent preference for particular prey types. If a predator concentrates its attack on the more abundant prey type the frequency of this prey type relative to other prey types will alter. The predator might then change its feeding to concentrate on another prey type when it became the most abundant - called 'apostatic selection' by Clarke (1962) or 'switching' by Murdoch (1969).

'Anti-apostatic selection' is a preference for the rare prey types (Greenwood, 1984) and may be the result of the rare prey type being easier to detect or to attack.

If a prey species is cryptic, a predator may overlook it and feed on other prey types. However, it may have a chance encounter with a cryptic individual and, perhaps as a result of a number of encounters, may 'learn to see' the cryptic prey and then 'selectively attend' that type of cryptic prey. The term 'searching image' was used by L. Tinbergen (1960) to describe this behaviour. He studied the population dynamics of a number of insect species in pinewoods and the proportions of each prey species in the food that adult great tits (*Parus major*) took to their young. He found that the proportions of the prey types in the nestlings' food did not reflect the proportions in the populations from which the parents were foraging. In fact, as particular prey type became available to the birds (usually because larvae had moulted into an instar stage that was large enough to be profitable to them) there was a time lag between the appearance of the prey in the environment and the appearance of the prey in the tits' diet. Tinbergen hypothesised that as the prey frequency increased so the number of prey the birds might come across by chance became greater and as a result the birds "adopted a specific searching image" for that prey type. The strict definition of the term 'search image' is "a perceptual change in the ability of a predator to detect familiar cryptic prey" (Lawrence and Allen, 1983), but it has been misused by many authors (for a review see Lawrence and Allen, 1983). As an adaptive behaviour, the use of search image by a predator might enable it to find cryptic prey more efficiently if it concentrated on only one prey type. Evidence for search images can be found in the work of Dawkins (1971a), Pietrewicz and Kamil (1979, 1981), Lawrence (1985a,b) and Gendron (1986) (see also review in Krebs, 1973 of earlier studies).

Another foraging behaviour that might affect prey populations is the preference shown by many predators for food types with which they are familiar over those which are novel (Coppinger, 1969, 1970). This can result in overpredation of the familiar food type (Allen and Clarke, 1968; Allen, 1974, 1984; Croze, 1970; Harvey, Birley and Blackstock, 1975; Raymond, 1984).

Any of the foraging behaviours by predators discussed in Section 1.6 may result in selection against particular prey population distributions and in selection against particular prey types.

1.7 AIMS AND PLAN OF EXPERIMENTS

1.7.1 Aims

The aims of this project were:

1. To test whether striped colour patterns confer a selective advantage in cryptic prey.
2. To study whether predators behave in such a way that would maintain a polymorphism in prey that have a colour pattern polymorphism that includes a striped colour pattern.

1.7.2 PLan of Experiments

The ideal experimental system for the study of protective coloration and frequency-dependent selection might be thought to be that of a real prey population in its natural situation and the effects upon it of its natural predators. However, difficulties exist in the use of this 'ideal' system because accurate observations may be impossible with many species of prey or predator, and, therefore, many experiments on visual selection by predators have used captive predators with prey in controlled situations (Sumner, 1934; De Ruiter, 1952; Kettlewell, 1955; Rabinowitch, 1968; Capretta, 1969; Coppinger, 1969, 1970; Dawkins, 1971a,b; Mueller, 1971; Manly, Miller and Cook, 1972; Bryan, 1973; Alcock, 1973; Kettlewell and Conn, 1977; Ohguchi, 1978; Pietrewicz and Kamil, 1977, 1979; Willis *et al.*, 1980; Gillis, 1982; Mikkola, 1984; Lawrence, 1985a,b; Gendron, 1986), or have used 'mark-recapture' techniques, in which precise knowledge of the fate of the prey was unknown (Kettlewell, 1955, 1956; Matthews, 1971), or have compared the proportions of predated indivduals with the proportions found in the wild or in artificially created populations (Arnold, 1966; Carter, 1968; Bowers, Brown and Wheye, 1985). Field experiments on the effects of predation on morph frequencies are rare, although some have been attempted (Sheppard, 1951; Cain and Sheppard, 1954; Kettlewell, 1955; Hughes and Mather, 1986).

The use of artificial prey in experiments on visual selection has been well argued by Allen (1973) and, together with the use of wild birds in their natural surroundings, he suggests that this experimental system is a valid one. Such an experimental system has been used successfully by many researchers on visual selection (Turner, 1961; Allen and Clarke, 1968; Morrell and Turner, 1969; Croze, 1970; Murton, 1971; Allen, 1972, 1973, 1974, 1976, 1984; Horsley *et al.*, 1979; Allen and Anderson, 1984; Cooper, 1984a,b; Lawrence, 1985c) and it was found to be valuable in the experiments in which it was used in this thesis.

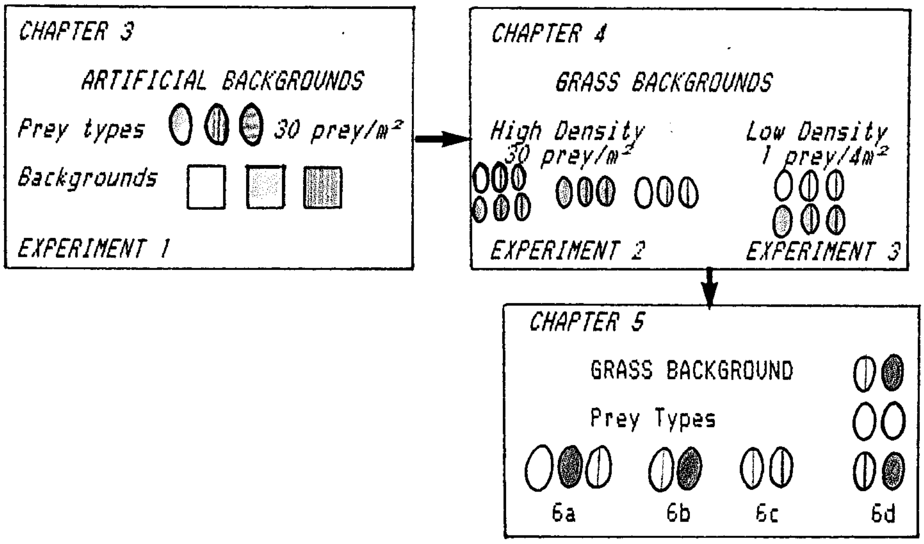
The approach was essentially simple: birds were offered choices between prey differing in their colour patterns. The ultimate effects on the prey selection were studied. Artificial prey made from a mixture of flour and lard and coloured with food dyes were used for the majority of experiments. Artificial backgrounds were used in the first experiment and then the design was modified to use the more natural background of a cut lawn. Wild garden birds were the predators in all but one of the experiments, when domestic chicks were used because strict control of individual experience was required.

Most studies on the functions of animal colour patterns in palatable animals have been descriptive (Poulton, 1890; Cott, 1940; Norris and Lowe, 1964) or have studied palatability (eg., Jones, 1932, 1934), resting site behaviour (Sargent, 1969a,b, 1978; Kettlewell and Conn, 1977; Mikkola, 1984) and the evolution of aposematic coloration (Coppinger, 1969, 1970). Only a few have studied crypsis directly (eg., Sumner, 1934 with fish; Carrick, 1936 and Mariath, 1982 with caterpillars; Kettlewell, 1955, 1956 with *Biston betularia*). Few of these experiments have involved striped colour patterns (see also Section 1.4).

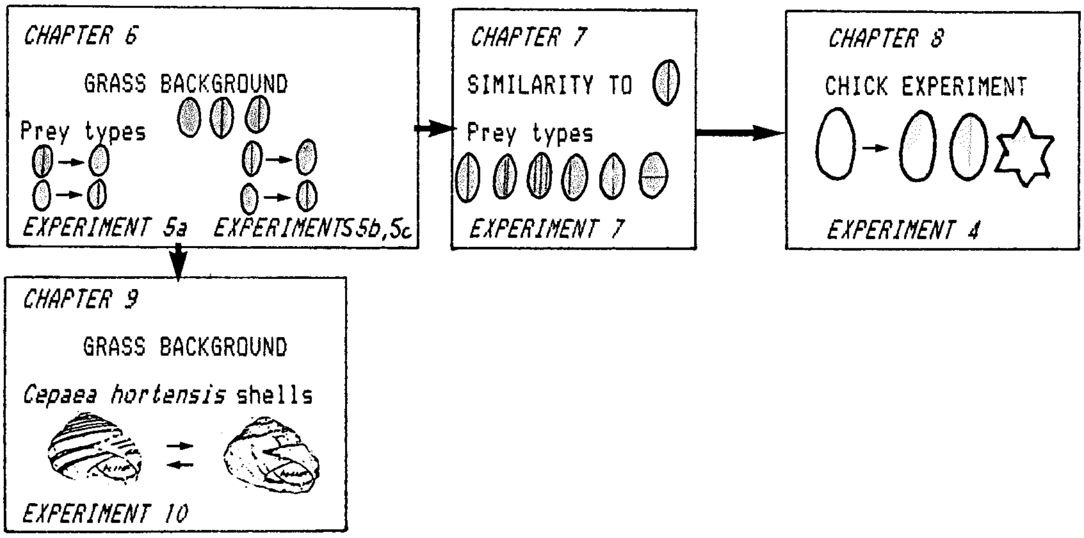
Turner (1961) used artificial prey for the first time in the study of protective coloration. He made the prey from flour and lard dough that was coloured with food dye and he presented them on a lawn to wild birds. One of the prey types was green with a fawn dorsal stripe. He found that the striped prey type was eaten significantly less than the plain models. Allen and Clarke (1968) followed Turner's method in using 'pastry' prey for their experiments on apostatic selection; but all their prey types, as well as those of Allen and other workers in subsequent experiments experiments with pastry prey, have been plain in colour.

TABLE 1.2: Summary of experiments and their corresponding chapters.

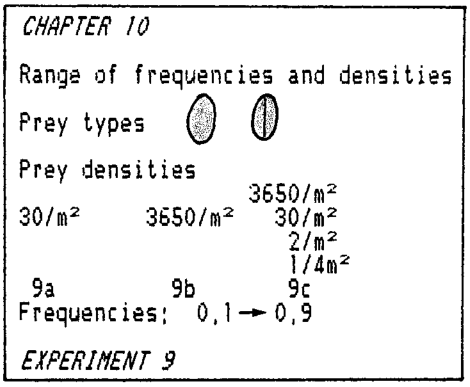
CHOICE TESTS



TRAINING EXPERIMENTS



VARIABLE FREQUENCY EXPERIMENTS



The first experiments reported in this thesis are concerned with crypsis. These were simple choice tests and tested the preferences of wild birds for prey colours and patterns on different backgrounds and at different densities. Subsequent experiments were extended to include studies on frequency-dependent selection on a polymorphic prey population, since many species are polymorphic for the presence or absence of stripes or bands (see Sections 1.5 and 1.6).

Training experiments of the type used by Allen and Clarke (1968) were performed to see if the birds acquired preferences for familiar prey which differed only in the presence or absence of a coloured stripe. Following this, the experimental design of Harvey *et al.* (1975) was modified and banded and unbanded shells of *Cepaea hortensis* were used as 'semi-natural' prey for further training experiments.

Finally, a range of different prey densities and frequencies was used in a series of experiments with the pastry prey to examine further frequency-dependent and density-dependent prey selection.

A list of experiments and their corresponding chapters is given in Table 1.2.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 INTRODUCTION

This chapter deals with the general materials and methods used in the ten experiments. Materials and methods that are specific to different experiments will be given in the relevant chapters.

The usual approach was to present bird predators with polymorphic populations of artificial prey; a method that has been used in the past by many researchers (for example: Turner, 1961; Allen and Clarke, 1968; Allen, 1972, 1973, 1974, 1976, 1984; Manly, Miller and Cook, 1972; Cook and Miller, 1977; Horsley, 1978; Cooper, 1984a,b). Evidence of selection on these 'prey' should emerge from statistical analysis of the proportions eaten.

Usually, the predators were wild birds in their natural habitats; thus the experimental design was close to that of natural predators exploiting prey. However, in one experiment (Experiment 4, Chapter 8), where it was necessary to control individual experience, domestic chickens were used.

Artificial prey made from pastry dough were used in most of the experiments. This type of 'prey' had a number of advantages over natural prey (*cf.* Cooper, 1984b):

i) they could be made in any size, shape or colour;
ii) they are immobile;
iii) they are unfamiliar to predators (except under known situations);
iv) it is possible to produce large numbers of identical types.

One experiment (Experiment 10, Chapter 9) used *Cepaea hortensis* shells filled with pastry (*cf.* Harvey, Birley and Blackstock, 1974). These could be considered as a semi-artificial prey. They were

TABLE 2.1: List of bird species acting as predators.

COMMON NAME	SCIENTIFIC NAME
Blackbird	*Turdus merula* L.
House sparrow	*Passer domesticus* (L.)
Starling	*Sturnus vulgaris* L.
Robin	*Erithacus rubecula* Hart.
Woodpigeon	*Columba palumbus* L.
Blue tit	*Parus caeruleus* L.
Great tit	*Parus major* L.
Feral pigeon	*Columba livia* Brisson
Collared dove	*Streptopelia decaocto* L.
Chaffinch	*Fringilla coelebs* L.
Magpie	*Pica pica* (L.)
Song thrush	*Turdus philomelos* Brehm.
Dunnock	*Prunella modularis* (L.)
Jay	*Garrulus glandarius* L.
Greenfinch	*Carduelis chloris* (L.)
Domestic chicken	*Gallus gallus* L.

comparable to the pastry prey in that they were immobile and their presentation could be controlled.

2.2 BIRD PREDATORS

Garden birds were used in all experiments except one, where domestic chickens were used. A list of the bird species is given in Table 2.1.

2.3 PREY

The artificial prey used in most experiments were made from pastry dough consisting of plain flour and lard in the ratio 12:5 by weight (modified from Turner, 1961). The pastry was coloured using food dyes (Pointings Ltd., Northumberland).

The pastry was rolled out between two sheets of paper dressing towels using a wooden rolling pin to a thickness of 2mm and the prey were cut out using a metal, specially made, pastry cutter. Two shapes were used: an oval and a star; most experiments (Experiments 1, 2, 3, 5, 6, 7, 8 and 9) involved only the oval prey type. The star-shape was used in Experiment 4, Chapter 8. Both prey shapes had approximately the same upper surface areas: oval - 172mm^2, star - 170mm^2. The ovals were 20mm long, 13mm wide; the stars were 20mm from point to point (Figure 2.1).

Colour patterns were applied to the upper surfaces of some of the prey. Except for the colour patterns on six prey types in Chapter 5, striped patterns were drawn on to the pastry using a felt pen filled with undiluted food dye. The felt pen ("Platignum Painting Stick"), which had contained water-soluble, non-toxic ink, was thoroughly washed out and the absorbent stick inside injected with food dye of the required colour. The stripe drawn, using a ruler, was 2mm wide. For the six prey types used in Chapter 5, the food dye was applied with a

TABLE 2.2: List of: 'pastry' prey types used; food dye added to 1000g uncoloured pastry to produce the different prey ground colours and the Munsell Color (1967) scores for Hue, Value/Chroma; descriptions of prey colour patterns and the food dye used for their application.

CHAPTERS	PREY TYPES	PLATES	FOOD DYE/1000g PASTRY (Pointings Ltd, Northumberland)	MUNSELL (1967) COLOUR SCORES FOR PREY GROUND COLOUR		PREY COLOUR PATTERN / FOOD DYE
				HUE	VALUE/CHROMA	
3	P	3,1 & 3,2	4ml Pea green (K6026)	10GY	7/6	Plain
	3LS	"	"		"	3 Longitudinal stripes Dark chocolate brown (K6097)
	3TS	"	"		"	3 Transverse stripes Dark chocolate brown (K6097)
4,6,7,10	G	4,1	10ml Apple green (K6027) 2ml Pea green (K6026) 4ml Coffee brown (K6098)	5GY	4/4,5	Plain
	GG	"	"		"	1 green longitudinal stripe 4ml apple green; 1ml pea green;1ml coffee brown
	GR	"	"		"	1 red longitudinal stripe Strawberry red (K6020)
	W	"	Uncoloured pastry	2,5Y	9/2	Plain
	WG	"	"		"	1 green longitudinal stripe (as for GG)
	WR	"	"		"	1 red longitudinal stripe (as for GR)
5	W,WR,WG	"	as above			
	R	5,1	Uncoloured pastry	2,5Y	9/2	Painted red over upper surface Strawberry red (K6020)
	WDR	5,1	"		"	Dark red stripe (see chapter for details)
	B	5,2	"		"	Painted blue over upper surface; Blue (K6023)
	WB	5,2	"		"	Blue stripe, Blue (K6023)
	Y	5,3	"		"	Painted yellow over upper surface; Egg yellow (K6013)
	WY	5,3	"		"	Yellow stripe Egg yellow (K6013)
8	W	4,1	as above			
	YS	-	10ml Lemon yellow (K6011)	5Y	8/10	Plain star
	YO	-	"		"	Plain oval
	YY	-	"		"	Yellow stripe, Yellow (K6013) on oval

fine artist's paint brush and was either painted over the entire upper surface of the rolled out pastry for the plain coloured prey types or stripes of the food dye were drawn that were 2mm wide. The use of a paint brush in the application of the food dye resulted in much stronger colours than by the use of the felt pen. After the colour pattern had been applied, the prey were cut out using the appropriate pastry cutter. A list of the prey types used in each chapter, together with the food dyes used for prey ground colours and for the colour patterns, is given in Table 2.2.

This flat design used for the prey was favoured because it meant that coloured patterns were relatively easy to apply in comparison with the cylindrical designs used in past experiments (eg., Turner, 1961). The oval shape is bilaterally symmetrical and this quality gave possibilities of varying the colour patterns in order to present the birds with, for example, both longitudinal and transverse striped prey. The star shape was used in only one experiment and was chosen because it was deemed to be 'opposite' in shape to the oval - a necessary requirement in this particular experiment. No colour patterns were drawn on the star-shaped prey.

The prey were of a size that were manageable to the author, especially with regard to the application of the colour patterns. The prey were also 'manageable' to the birds: all species could carry them away, and the larger species could eat them whole.

Water affected the colours of the prey and caused the patterns to run. This meant that experiments could not be carried out in heavy or prolonged rain.

Cepaea hortensis shells filled with pastry were used in Experiment 10, and will be discussed in the relevant chapter (Chapter 9).

2.4 BACKGROUNDS

Most of the experiments (Experiments 2, 3, 5, 6, 7, 8, 9 and 10) used grass lawns as the backgrounds for the prey. The sites were in gardens in and around Southampton and Bristol, Great Britain. These grass backgrounds differed from site to site, both as to composition of the plants found and to the length of grass. To the human eye, all prey were more conspicuous on well-mown lawns than on uncut ones. Within sites there were also variations due to the weather. Rain or drought particularly affected the colour of the grass. However, these variations are those that natural prey would experience io the wild.

Experiment 1, Chapter 3, used painted plywood boards as backgrounds. Details are given in Chapter 3, Section 3.2.2.

Dyed canvas squares were used as controls for background in Experiment 2. These were squares, one metre by one metre, of primed canvas coloured a pink-brown with fabric dyes ("Screen and Fabric Printing Colour", Rowney, England).

2.5 METHODS

Since many different types of prey population were presented in the different experiments, it is not possible to go into great detail in this chapter as to the methods of presentation. However, some general points can be made at this juncture.

2.5.1 Density

In total, four different prey densities were used:

Density prey/m^2	**Experiments**	**Chapters**
3850	9b, 9c	10
30	1, 2, 4, 6, 8, 9a, 9c	3, 4, 8, 5, 10
2	5, 7, 9c, 10	6, 7, 10, 9
0.25	3, 9c	4, 10

The density of 3850 prey/m^2 was called the 'maximum' density because it was the result of placing the oval prey so that they were all touching, without any overlapping.

2.5.2 Population Size

Population sizes for Experiments 1, 2, 3, 4, 6, 9c[1prey/4m^2] and 10 were 30 prey. A prey population size of 60 was used in Experiments 7, 9a, 9b and 9c[3850prey/m^2, 30prey/m^2, 2prey/m^2]. Various prey population sizes were used in Experiments 5a and 5c because of the areas of grass lawn available for the experiments: the range of prey populations was 24 prey - 100 prey. The population size in Experiment 5b was 100 prey.

2.5.3 Prey distributions

At the maximum density (3850/m^2), individual prey were drawn at random from a box and were placed, pattern uppermost, on the grass so that their edges were touching as much as possible. The procedure was repeated until the appropriate number of each prey type had been placed. The final prey population was circular in distribution.

The density of 30 prey/m^2 used prey population sizes of 30 or 60, depending on whether an experimental area of 1m^2 or 2m^2 was used. Prey were scattered at random over the area and then adjusted so that their colour patterns were uppermost, were not overlapping and were not hidden in the grass.

Prey densities 2/m^2 and 1/4m^2 used various prey population sizes depending on what experimental area was used. Randomisation of the prey populations was more complicated than for the two higher densities. The experimental plots were marked out with tent pegs on the lawns in metre-squares or in 2 x 2 metre-squares. Copies of the grids were made with each square divided into four quarters, and these copies were used to record the distributions of the future prey populations. To avoid the effects of the birds not searching uniformly over the areas, the grids were divided into smaller areas that were allotted equal numbers of the prey types. At first the procedure for randomisation of the populations used playing cards; subsequently computer programs were written that also printed out copies of the distribution (General Appendix A). Further details are given in the appropriate chapters.

CHAPTER 3

EXPERIMENT 1: CHOICE TESTS ON ARTIFICIAL BACKGROUNDS - Are artificial prey at an advantage on matching backgrounds?

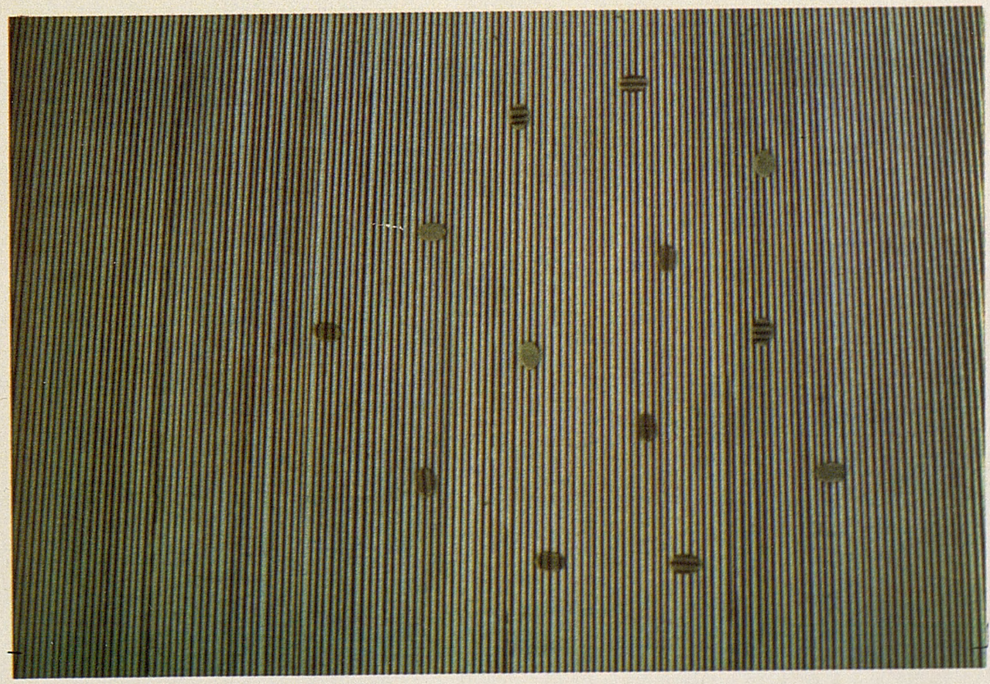
3.1 INTRODUCTION

The first set of experiments reported in this thesis investigated crypsis and colour patterns and were choice tests of different prey types presented to wild birds. Using prey types that differed only in their colour patterns, the aim of this first experiment was to investigate whether the bird predators would select unmatching prey presented on two-dimensional backgrounds. This approach has been used by researchers in the past with limited success. Cooper (1984a) presented plain prey of two colours on flat backgrounds, and Sellers (1980) presented striped and unstriped prey on flat backgrounds to garden birds. In both these experiments more unmatching prey were eaten than matching prey. It was hoped that this experimental design of using flat backgrounds in experiments with artificial prey would provide a useful one for future investigations since changes in background colour patterns would be very easy and the same backgrounds could be used at different sites.

Wild birds were given paired choices between three types of plain and striped artificial prey presented on plain or striped flat backgrounds. Two striped prey types were used in order to see whether the direction of a striped pattern had any effect on the preferences of the bird predators. On the striped background, orientation of the prey was also taken into consideration; it is thought that, in some cryptic prey, selection by visually hunting predators has resulted in genetic control over resting attitudes so that the prey choose a matching background and some even orientate themselves to match the background pattern (Sargent, 1969a,b; Kettlewell and Conn, 1977; but see also Mikkola, 1984).

PLATE 3.1: Experiment 1, Series 2. The three prey types on the plain green background. From the top, in clockwise order: 3LS, 3TS, P.

PLATE 3.2: Experiment 1, Series 3. The three prey types on the striped background, showing the different prey orientations used.



3.2 MATERIALS AND METHODS

3.2.1 Prey

The prey were the three oval 'pea green' prey types made from pastry dough described in Chapter 2, Table 2.2: Plain green (**P**), green with three longitudinal stripes (**3LS**) and green with three transverse stripes (**3TS**). (Plates 3.1 and 3.2)

3.2.2 Backgrounds

Three backgrounds were made from 0.5 inch plywood board. These were 1m x 1m squares: two green and one white. Of the two green boards, one was plain while the other had brown stripes drawn on it (Plates 3.1 and 3.2). To the human eye the colour of the two green boards matched the green of the prey. "Rowney" hardboard primer was used to prime the boards before painting. "Dulux Vinyl Brilliant White" emulsion paint was used to paint the white board, and also used as an undercoat for the green boards. A mixture of the white emulsion paint and water-soluble powder paints (Winsor and Newton New Art Powder Colour, Brilliant Green) was used for painting the green boards. Brown stripes, which were the same width and distance apart as those of the striped prey (2mm wide and 2mm apart), were drawn, using a metre rule, on one of the green boards with a felt pen containing brown permanent ink (Edding 3000). The resulting stripes were, to the human eye, a good match to those on the striped prey.

The use of the white board was designed to provide information on any preferences the birds might have had for any of the three prey types in the absence of a match between prey and background.

3.2.3 Predators

The predators were all wild garden birds. Table 3.1 gives a list of the species of birds observed feeding and on which backgrounds, together with approximate numbers of each birds species.

TABLE 3.1: Experiment 1 - species of birds observed feeding on each background (estimated numbers of birds in parenthesis). A plus sign indicates the presence of that species. For scientific names see Chapter 2, Table 2.1.

Species		BACKGROUND White	Plain	Striped
Blackbird	(2)	+	+	+
Blue tit	(5+)	+	+	+
Great tit	(2+)	+	+	+
Woodpigeon	(1)	+	+	+
Robin	(2)	+	+	-
Chaffinch	(1)	-	-	+

3.2.4 Procedure

a) General

Prior to the start of the experiments, a piece of unpainted board (approximately 0.5m x 0.3m) was placed on grass close to some bushes at the experimental site at the Medical and Biological Sciences Building at the University of Southampton (O.S. grid reference: SU 418156). It was scattered with bread and wild bird food in order to familiarise the birds with feeding from a board on the ground. Initially, many birds showed reluctance in feeding from the board and this 'pre-experimental feeding' saved delay at the start of the experiment proper.

The birds were presented with a population of 30 prey scattered at random over one of the experimental backgrounds. The populations were made up of two of the three prey types: 15 of each.

b) Series 1 - White background

The white background was used first in order to test for any preferences by the birds for any of the prey types.

This series ran for three days with a different pair of prey presented on each day. The order of presentation of the three pairs was determined randomly. The prey were dropped on to the board at random. Their positionings were then adjusted slightly so that they did not overlap and so that their colour patterns faced uppermost. The birds were allowed to feed and predation was stopped when approximately half of the prey had been taken. The remaining prey were then scored. Initially, it was decided to obtain five replicates in a day, but the low rate of predation meant that this was not possible, and so the series was repeated. An increase in the predation rate in the repeat series meant that six replicates per day were obtained. This series ran from 9th - 17th November 1981.

c) Series 2 - Plain green background- Plate 3.1

This series ran for three days (16th - 18th February 1982) with five replicates per day. The method of presentation was the same as for Series 1. There was no repetition of the series.

TABLE 3.2: The twelve prey orientations used in Experiment 1, Series 3 and the order in which they were presented. Prey with longitudinal axes parallel to the stripes on the background are represented by ↑ and prey with longitudinal axes at right-angles to the stripes on the background are represented by →.

PREY TYPES		PREY ORIENTATION		ORDER OF PRESENTATION
P	3TS	↑	↑	10
P	3LS	↑	↑	5
3LS	3TS	↑	↑	11
P	3TS	↑	→	2
P	3LS	↑	→	8
3LS	3TS	↑	→	1
P	3TS	→	→	9
P	3LS	→	→	6
3LS	3TS	→	→	3
P	3TS	→	↑	7
P	3LS	→	↑	12
3LS	3TS	→	↑	4

d) Series 3 - Striped green background - Plate 3.2

This series ran from 9th March - 2nd April 1982.

The procedure was essentially the same as in Series 1 and 2, but the direction of the prey in relation to the stripes on the background was taken into consideration. The potential positions of the prey were limited to resting with the longitudinal axis either parallel or at right angles to the stripes on the board. This resulted in each of the two striped prey types having their stripes parallel to the stripes on the background in half the trials. Further, to obtain the maximum match between the striped prey with patterns parallel to those of the background and the background, the prey were moved slightly so that the stripes of the prey lay exactly over those of the background. Twelve prey combinations were done (Table 3.2). An arrow pointing upwards placed after the prey type abbreviation represents prey orientated with the longitudinal axis parallel to the stripes on the background (eg. **P↑**) and an arrow pointing to the right represents prey orientated at right angles to the stripes of the background (eg. **3LS→**).

3.3 RESULTS

The results are given in Tables 3.3, 3.4 and 3.5 together with the results from G tests (Sokal and Rohlf, 1981).

There were no statistically significant preferences for any of the three prey types in the white background series or in the plain green background series. Overall, there were no significant preferences for any of the prey types in the striped background series, except in prey combinations **P↑/3LS↑** and **P↑/3LS→**, where consistently more plain prey (**P**) were eaten than striped prey.

If the results from series 3 for each prey combination, regardless of prey orientation, are grouped together, then in the **P/3LS** trials the plain prey were eaten consistently more than the longitudinally striped prey ($p<0.01$, Wilcoxon matched-pairs signed-ranks test).

TABLE 3.3: Series 1 – White Background
Numbers of each prey type eaten in each of the replicates in Experiment 1, Series 1, with values of G for a departure from a 1:1 expectation (G and G_T) and for heterogeneity within each set of replicates (G_H). None of the values of G were statistically significant. Series 1 was repeated once, the two groups being separated by a dotted line.

Table 3.3a: P/3TS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN P	3TS	TOTAL	$G_{(1)}$
1	8	6	14	0.287
2	8	6	14	0.287
3	14	10	24	0.670
TOTAL	30	22	52	1.236
$G_{T(3)} = 1.243$, $G_{H(2)} = 0.008$				
……				
4	8	7	15	0.068
5	8	6	14	0.287
6	7	9	16	0.251
7	7	9	16	0.251
8	6	9	15	0.604
9	6	8	14	0.287
TOTAL	42	48	90	0.400
$G_{T(6)} = 1.746$, $G_{H(5)} = 1.345$				

Table 3.3b: P/3LS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN P	3LS	TOTAL	$G_{(1)}$
1	9	5	14	1.159
2	11	10	21	0.048
3	8	7	15	0.067
TOTAL	28	22	50	0.722
$G_{T(3)} = 1.273$, $G_{H(2)} = 0.552$				
……				
4	7	8	15	0.067
5	6	9	15	0.604
6	7	9	16	0.251
7	10	6	16	1.011
8	7	8	15	0.067
9	9	8	17	0.059
TOTAL	46	48	94	0.043
$G_{T(6)} = 2.058$, $G_{H(5)} = 2.015$				

Table 3.3c: 3LS/3TS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	3LS	3TS		
1	5	8	13	0.699
2	6	9	15	0.604
3	8	7	15	0.067
4	6	6	12	0.455
TOTAL	25	30	55	0.455
$G_{T(4)} = 1.369$, $G_{H(3)} = 0914$				
………………				
5	12	7	19	1.331
6	9	7	16	0.251
7	6	9	15	0.604
8	8	11	19	0.476
9	7	8	15	0.067
10	7	9	16	0.251
TOTAL	49	51	100	0.040
$G_{T(6)} = 2.979$, $G_{H(5)} = 2.939$				

TABLE 3.4: Series 2 - Plain Green Background
Numbers of each prey type eaten in eah of the replicates in Experiment 1, Series 2, with values of G for a departure from a 1:1 expectation (G and G_T) and for heterogeneity within each set of replicates (G_H). None of the values of G were statistically significant.

Table 3.4a: P/3TS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	P	**3TS**		
1	8	7	15	0.067
2	8	6	14	0.287
3	5	9	14	1.159
TOTAL	21	22	43	0.023

$G_{T(3)} = 1.512$, $G_{H(2)} = 1.489$

Table 3.4b: P/3LS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	P	**3LS**		
1	6	7	13	0.077
2	8	6	14	0.287
3	6	8	14	0.287
4	7	7	14	0.000
5	9	7	16	0.251
TOTAL	36	35	71	0.014

$G_{T(5)} = 0.901$, $G_{H(4)} = 0.887$

Table 3.4c: 3LS/3TS

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	3LS	**3TS**		
1	7	8	15	0.067
2	6	6	12	0.000
3	11	6	17	1.493
4	7	8	15	0.067
5	9	9	18	0.000
TOTAL	40	37	77	0.117

$G_{T(5)} =1.626$, $G_{H(4)} = 1.509$

TABLE 3.5: Series 3 - Striped Green Background
Numbers of each prey type eaten in each of the replicates in Experiment 1, Series 3, with values of G for a departure from a 1:1 expectation (G and G_T) and for heterogeneity within each set of replicates (G_H). None of the values of G were statistically significant.

Table 3.5a: P↑/3TS↑

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN **P↑**	 **3TS↑**	TOTAL	$G_{(1)}$
1	6	6	12	0.000
2	6	5	11	0.091
3	5	6	11	0.091
4	5	7	12	0.335
5	7	7	14	0.000
TOTAL	29	31	60	0.067

$G_{T(5)} = 0.517$, $G_{H(4)} = 0.450$

Table 3.5b: P↑/3TS→

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN **P↑**	 **3TS→**	TOTAL	$G_{(1)}$
1	7	6	13	0.077
2	7	7	14	0.000
3	9	6	15	0.604
4	4	6	10	0.403
TOTAL	27	25	52	0.077

$G_{T(4)} = 1.084$, $G_{H(3)} = 1.007$

Table 3.5c: P→/3TS→

REPLICATE	NUMBER OF EACH PREY TYPE EATEN **P→**	 **3TS→**	TOTAL	$G_{(1)}$
1	5	5	10	0.000
2	7	6	13	0.077
3	7	4	11	0.829
4	5	5	10	0.000
5	10	8	18	0.223
TOTAL	34	28	62	0.582

$G_{T(5)} = 1.128$, $G_{H(4)} = 0.547$

Table 3.5d: P→/3TS↑

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	P→	**3TS↑**		
1	6	6	12	0.000
2	8	7	15	0.067
3	4	6	10	0.403
4	11	8	19	0.476
5	10	9	19	0.053
TOTAL	39	36	75	0.120

$G_{T(5)} = 0.998$, $G_{H(4)} = 0.878$

Table 3.5e: P↑/3LS↑

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	P↑	**3LS↑**		
1	5	5	10	0.000
2	6	4	10	0.403
3	7	6	13	0.077
4	6	4	10	0.403
5	7	6	13	0.077
TOTAL	31	25	56	0.644

$G_{T(5)} = 0.959$, $G_{H(4)} = 0.315$

Table 3.5f: P↑/3LS→

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN		TOTAL	$G_{(1)}$
	P↑	**3LS→**		
1	6	4	10	0.403
2	7	3	10	1.646
3	6	4	10	0.403
4	9	6	15	0.604
5	10	8	18	0.223
TOTAL	38	25	63	2.702

$G_{T(5)} = 3.278$, $G_{H(4)} = 0.576$

Table 3.5g: P→/3LS→

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN P→	3LS→	TOTAL	$G_{(1)}$
1	6	6	12	0.000
2	6	4	10	0.403
3	8	6	14	0.287
4	10	9	19	0.053
5	9	10	19	0.053
TOTAL	39	35	74	0.216

$G_{T(5)} = 0.795$, $G_{H(4)} = 0.578$

Table 3.5h: P→/3LS↑

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN P→	3LS↑	TOTAL	$G_{(1)}$
1	8	8	16	0.000
2	5	5	10	0.000
3	5	6	11	0.091
4	8	10	18	0.223
5	9	9	18	0.000
TOTAL	35	38	73	0.123

$G_{T(5)} = 0.314$, $G_{H(4)} = 0.190$

Table 3.5i: 3LS↑/3TS↑

REPLICATE	NUMBERS OF EACH PREY TYPE EATEN 3LS↑	3TS↑	TOTAL	$G_{(1)}$
1	5	6	11	0.091
2	5	5	10	0.000
3	6	7	13	0.077
4	7	7	14	0.000
5	8	10	18	0.223
TOTAL	31	35	66	0.243

$G_{T(5)} = 0.391$, $G_{H(4)} = 0.148$

Table 3.5j: 3LS↑/3TS→

	NUMBERS OF EACH PREY TYPE EATEN			
REPLICATE	3LS↑	3TS→	TOTAL	$G_{(1)}$
1	7	9	16	0.251
2	9	5	14	1.159
3	6	8	14	0.287
4	4	8	12	1.359
TOTAL	26	30	56	0.286

$G_{T(4)}$ 3.056, $G_{H(3)}$ = 2.770

Table 3.5k: 3LS→/3TS→

	NUMBERS OF EACH PREY TYPE EATEN			
REPLICATE	3LS→	3TS→	TOTAL	$G_{(1)}$
1	6	9	15	0.604
2	7	5	12	0.335
3	12	11	23	0.044
4	5	6	11	0.091
5	10	10	20	0.000
TOTAL	40	41	81	0.012

$G_{T(5)}$ =1.074, $G_{H(4)}$ = 1.061

Table 3.5l: 3LS→/3TS↑

	NUMBERS OF EACH PREY TYPE EATEN			
REPLICATE	3LS→	3TS↑	TOTAL	$G_{(1)}$
1	6	7	13	0.077
2	5	7	12	0.335
3	8	6	14	0.287
4	7	6	13	0.077
5	10	10	20	0.000
TOTAL	36	36	72	0.000

$G_{T(5)}$ = 0.776, $G_{H(4)}$ = 0.776

Analysis of variance using arc-sine transformed percentages of prey eaten shows that there is heterogeneity between the two **P/3TS** repeats of Series 1 ($F_{(1,7)} = 6.99$, $p<0.05$) and no heterogeneity between the repeats of **P/3LS** ($F_{(1,7)} = 2.157$) or **3LS/3TS** ($F_{(1,8)} = 0.349$). This heterogeneity prevented the grouping of the results from the two **P/3TS** days together in statistical analysis, therefore they were treated separately.

Analysis of variance on the results from Series 3, shows that, for the **P/3TS** and **3LS/3TS** prey combinations, the different orientations of the prey did not significantly affect the proportions of the prey types eaten (**P/3TS**: $F_{(3,15)} = 0.822$, N.S.; **3LS/3TS**: $F_{(3,15)} = 0.229$, N.S.). In the **P/3LS** prey combinations, the orientation of the prey did affect the preferences of the birds ($F_{(3,16)} = 7.121$, $p<0.01$); the effect was on the magnitude rather than on the direction of the preferences since the direction is constant (see above).

ANOVA were also used to compare the results of each prey combination on the two plain backgrounds (Series 1 and Series 2). The backgrounds did not significantly affect the proportions of the prey types eaten (the **P/3TS** repeats of Series 1 treated separately - **P/3TS**: $F_{(1,4)} = 1.77$, $F_{(1,7)} = 0.1$; **P/3LS**: $F_{(1,12)} = 0.05$; **3LS/3TS**: $F_{(1,13)} = 1.0$). Since orientation was an additional factor in Series 3, direct comparison cannot be made between the results from striped background series and the plain background series.

3.4 DISCUSSION

With the plain green background, there is no evidence that the birds prefer the matching prey type.

With the striped background, the birds consistently preferred the plain prey type rather than the longitudinally-striped prey type, although this preference is not statistically significant within individual replicates.

Orientation of the prey types on the striped board affected the magnitude of the preference shown by the birds for the plain prey type. Surprisingly, this preference was at its greatest in the **P↑/3LS→** prey orientation, where the stripes of the **3LS** prey were at right-angles to the stripes of the board. There appears to be no obvious explanation for this particular result. The original prediction was that the prey type that appeared to most closely match the background should be taken the least. Although, on the striped background, the striped prey type matched the background 'better' than the plain prey type, this particular orientation of the striped prey type was not the 'best match' possible. A closer match was found, for example, in the **P→/3LS↑** prey orientation, but these replicates gave an overall result that indicated a slight preference for the striped prey. The only conclusion that can be drawn from the results is that the birds consistently took more plain prey but that the degree of this preference did not occur most strongly in the predicted prey orientations.

There is no evidence that the different plain backgrounds affected the preferences of the birds for any of the prey types. In the striped background series, unlike in the other two series, the prey could only lie in two directions in relation to the board and the orientation of the prey was shown to influence the birds' feeding preferences.

Cooper (1984a) performed a similar experiment using brown and green pastry discs (6.5mm diameter, 2mm thick) on brown and green flat backgrounds. He found no statistically significant evidence that the birds preferred unmatching prey, although the results were in the 'right' direction. He suggested that the birds might have been capable of detecting the prey due to shortcomings in the quality of the colour match between the prey and the background or that they might have been using cues in searching for their prey that were unrelated to colour. These cues could have been outline, depth and shadow. Certainly, to the human eye, the prey in the experiments reported in this chapter were visible, owing to their depth and shadows, especially in bright weather. Subjectively, the striped prey on the striped background were less visible than the plain prey on the plain green background: an observation that, to some extent, was borne out by the results from the experiments.

Sellers (1980) presented garden birds with white pastry discs (18mm diameter, 1mm thick) that were either plain or had a single central stripe (5mm wide) on plain and striped matching backgrounds. He investigated the effects of orientation as well as the effects of background matching. His results were much clearer than those of Cooper (1984a) and me. He found that the birds took more unmatching prey than matching prey when these were presented in equal numbers. Different orientations of the striped prey produced different degrees of predation. The striped prey type suffered the least predation when its stripe was parallel to the stripes of the background. However, the experimental design that Sellers used was different in many respects from my design and that of Cooper (1984a). In particular, the prey were thinner and this presumably reduced the amount of shadow that they threw on to the background and which the birds may have been using as a cue for finding the prey (see above). Fewer prey were presented on the boards and this may have increased the selectivity of the birds. The method of recording prey taken was also different: instead of a replicate being halted when approximately half the prey had been eaten, replacement of eaten prey occurred at 15-20 minute intervals until a total of approximately 100 prey had been taken. This method resulted in the proportions of the two prey types being maintained at close to their original value. If the birds had a preference for feeding in one particular area of the board (this behaviour was observed in my experiments, with the birds generally starting to feed from the side of the board nearest to the bushes), then any preference for one prey type might have been obscured if the birds were not stopped from feeding until as large a proportion as 50% of the prey were taken. If a trial is halted when only one or two prey have gone and then these prey replaced, as in Seller's experiments, then any consistent preference that the birds might show for one prey type may result in a significant difference between the final proportions of the two prey types eaten. For this reason it was decided that the design of most future experiments would incorporate frequent replacement of the eaten prey as opposed to cessation of trials when 50% of prey had been eaten.

Because of the above-mentioned problems, flat boards did not appear to be suitable as backgrounds for future experiments. Grass lawns have been used by many researchers for predation experiments of all kinds (for example, Turner, 1961; Allen, 1972, 1974, 1976, 1984; Smith, 1974b; Harvey, Birley and Blackstock, 1975; Horsley, Lynch, Greenwood, Hardman and Mosely, 1979) and it was felt that the natural three-dimensional background with its inbuilt 'stripy effect' would be a good background for most future experiments.

3.5 SUMMARY

1. This experiment was designed to test whether flat backgrounds could be used for the investigation of the responses of bird predators to the colour patterns of their prey.
2. It was hoped that, by varying the colours and patterns of the backgrounds in relation to the prey, it could be shown whether birds prefer the unmatching prey when given a choice between matching and unmatching prey.
3. No evidence was found for a preference for unmatching prey to be the case on a plain green background.
4. There were indications that, on a striped background plain prey were preferred over prey with longitudinal stripes regardless of the orientation of the prey to the stripes on the board; but the results were not clear.
5. The orientation of the prey relative to the stripes on the background affected the magnitude of the birds' preferences; but not in a predictable direction.
6. The use of flat boards as backgrounds for further work seemed, on the whole, to be unprofitable.

CHAPTER 4

EXPERIMENTS 2 & 3: CHOICE EXPERIMENTS AT TWO DENSITIES - Are striped matching prey at an advantage on lawn backgrounds?

4.1 INTRODUCTION

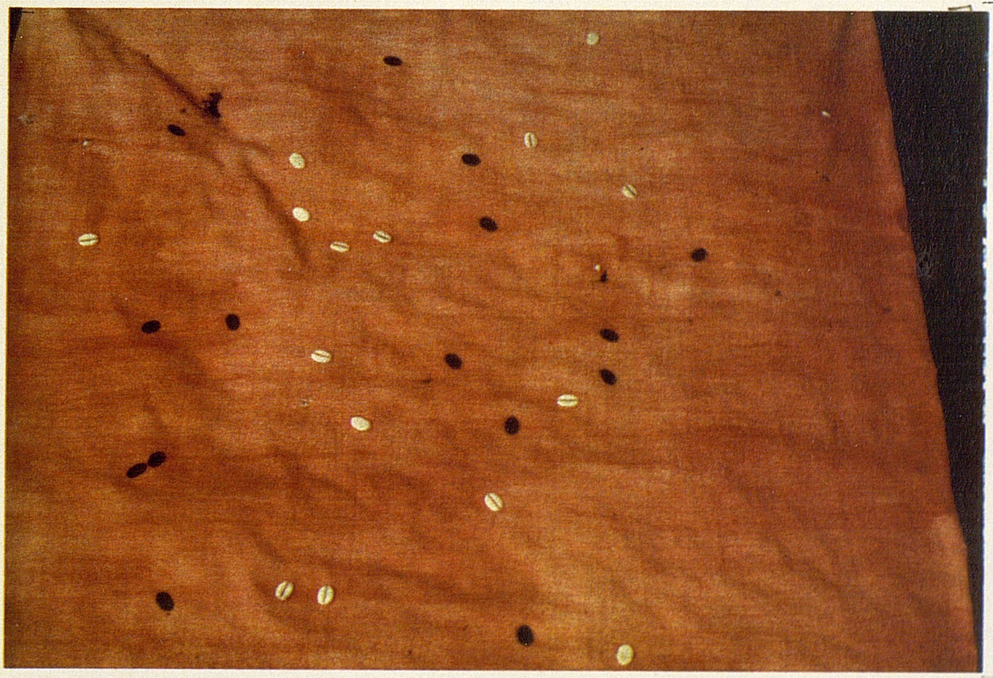
The experiments reported in this chapter follow on from the choice tests in Chapter 3 - artificial prey that appeared to match the background to different extents were presented to garden birds to investigate whether the birds preferred unmatching prey. The background used for these (and most subsequent experiments) was that of grass lawn. The design used in Chapter 3 was adapted for work on grass. A single stripe on the prey was used instead of three because this seemed to provide a better match to the grass leaves of the lawn background.

Six prey types were used, consisting of two prey ground colours (white and green) and three colour patterns (plain, green-stripe and red-stripe). The green ground colour was made to match the colour of the grass background; the green stripe matched a blade of grass in colour and width.

The prey were presented at two densities: 30 prey/m^2 (Experiment 2) and 1 prey/4m^2 (Experiment 3). The higher density of 30 prey/m^2 is the same as that used in the first experiment and was chosen for this reason. Tinbergen (1965) suggests that an important behavioural correlate to crypsis is living well spaced out (at inter-individual distances that greatly exceed the distance from which predators usually detect the prey readily). Tinbergen, Impekoven and Franck (1967) reported on an experimental study of the effects of spacing-out on the predation of cryptically-patterned eggs; the results suggest that spacing-out is of survival value whenever predators search intensively in a restricted area. Because many animals thought to be cryptic live at low densities (Edmunds, 1974) it was decided to present the experimental prey at densities low enough to make the predator search

PLATE 4.1: The six prey types used. From left to right, top row: G, GR, GG; bottom row: W, WR, WG.

PLATE 4.2: A 'population' of the six prey types on the canvas background.



for them. The density chosen was 1 prey/4m^2; the distance between prey would then average 2 metres, a distance great enough to eliminate the possibility of most species of bird seeing two prey at the same time (Croze, 1970; Smith, 1974b).

4.2 MATERIALS AND METHODS

4.2.1 Prey

The prey were six of the prey types described in Chapter 2: plain white (**W**), white with a green stripe (**WG**), white with a red stripe (WR), plain green (**G**), green with a green stripe (**GG**), and green with a red stripe (**GR**). (Plate 4.1.)

4.2.2 Backgrounds

All the experiments were carried out on areas of lawn at the Medical and Biological Sciences Building, Southampton University.

Control experiments for Experiment 3 used the canvas square described in Chapter 2, Section 2.4, pegged onto the area of lawn used for the rest of the experiments. (Plate 4.2.)

4.2.3 Predators

Table 4.1 gives a list of the species of birds observed feeding in the experiments.

4.2.4 Procedure - Experiment 2 (High Density)

a) General

Thirty prey were presented in an area of one square metre. The prey were scattered on the experimental area in the manner described in Chapter 3: they were dropped from waist-height and then adjusted so that their patterns were uppermost. The site was then watched and any predation observed was recorded listing species of bird feeding and for type of prey taken. Eaten prey were replaced until approximately 100

TABLE 4.1: Experiments 2 and 3 - species of birds observed feeding in each replicate. For scientific names see Table 2.1.

DENSITY	30 Prey/m^2																					1 Prey/4m^2					
SERIES	1								2						3												
BACKGROUND	Canvas				Grass				Canvas			Grass			Canvas				Grass			Grass					
YEAR	82		83		82		83		82	83		82	83		82		83		82	83		82		83			
REPLICATE	1	2	3	4	1	2	3	4	1	2	3	1	2	3	1	2	3	4	1	2	3	1	2	3	4	5	6
Blackbird	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+
Chaffinch	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	-	+	+	-	+	+	-	-	+	-	-	+
Starling	+	+	+	-	+	+	-	-	+	-	-	+	-	-	+	+	+	-	-	-	-	-	-	+	-	+	+
Robin	-	+	+	+	+	+	+	-	+	+	+	+	+	+	-	-	+	+	-	+	+	+	+	-	+	+	+
Woodpigeon	+	+	+	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Great tit	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blue tit	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+
Dunnock	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-
Feral pigeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
Songthrush	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	+	?	+
Collared dove	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<u>INDIVIDUAL BLACKBIRDS IN 1983</u>																											
Male A			+	+			+	+		+	+		+	+			+	+		+	+			+	+	+	+
Male B			+	+			+	+		+	+		+	+			+	+		+	+			-	+	+	+
Female Br			+	+			+	-		+	-		+	-			-	-		-	-			-	-	-	-
Female Y			-	-			-	-		-	+		-	+			-	-		-	+			+	+	+	+
Female Bl			-	-			-	-		-	+		-	-			-	-		-	-			-	-	-	-

had been taken. If more than 15 prey had been eaten before they could be replaced these results were excluded from the final analysis. If 100 prey had not been eaten during the course of one day the experiment was continued the following day or at the earliest opportunity.

The canvas square was used as a control for the effect of background. Each experiment using grass as the background was preceded by an equivalent experiment carried out on the canvas. This procedure controlled for changes in the birds' preferences for any of the prey types during the course of the experiments.

Three experimental series were executed with different combinations of the prey types: Series 1 - all six (**W**, **WG**, **WR**, **G**, **GG**, **GR**); Series 2 - G, **GG**, & **GR**; Series 3 - **W**, **WG**, & **WR**. Series 2 was performed because the results of Series 1 showed that the birds had a very strong preference for the white prey types and therefore it was difficult to establish any preferences the birds might have had for the green prey types. Series 3 repeated the design of Series 2 using the three white prey types to allow direct comparison with Series 2 during later analysis.

These experiments were first performed in the summer of 1982 and then repeated in the summer of 1983. The dates of the three series were as follows:

Series 1: 26th May - 14th June 1982
23rd May - 26th May 1983
Series 2: 15th June - 16th June 1982
31st May - 2nd June 1983
Series 3: 17th June - 28th July 1982
2nd June - 3rd June 1983

b) Series 1 - Presentation of all six prey types

Five of each prey type were presented. In 1982 this series was repeated once; and in 1983 it was also repeated once, making a grand total of four replicates.

c) Series 2 - Presentation of the three green prey types

Ten of each of the three green prey types were presented. In 1982 there was no replication, but in 1983 this series was repeated once, to make a grand total of three replicates.

d) Series 3 - Presentation of the three white prey types

Ten of each of the three white prey types were presented. In 1982 the control experiment on canvas was carried out twice before the experiment on grass because there were over two weeks of heavy rain showers after the first control experiment: any experiments during that time were prevented because the rain caused the artificial prey to change colour and caused the dye of the coloured stripe to run. It was felt that the time gap after the first canvas control would have been too great to allow direct comparison between it and the subsequent grass experiment and therefore the control was repeated. There was no replication of the grass experiment in 1982. In 1983 the series was repeated once. Therefore there were three complete replicates of this series with an additional control experiment.

4.2.5 Procedure - Experiment 3 (Low Density)

Five of each of the six prey types were presented in an area 10 metres by 12 metres. A grid was marked out in 1 metre squares with tent pegs on grass. The grid was divided into five blocks of six 2m x 2m squares. Within each block, one of each prey type was placed - one per 2m x 2m square.

An important consideration in the design of this experiment (and others) was the method for distribution of the prey population. It was essential to ensure not only a random prey distribution over the grid but also to ensure that there were no extreme groupings of particular prey types in any areas of the grid: so that if the birds visited one area of the grid more often than the rest, any disproportionate predation on one or more prey types would not be the result of the prey distribution. Therefore care was taken with the distribution of the prey.

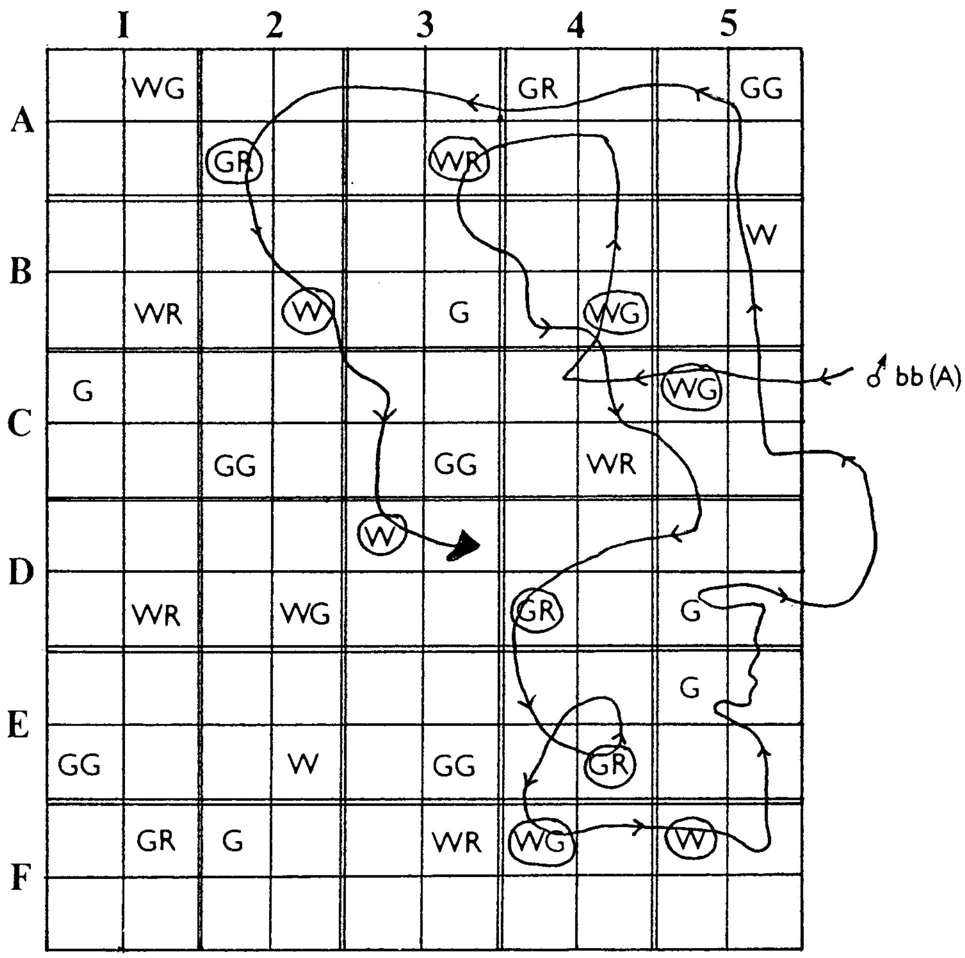
FIGURE 4.1: Experiment 3. Distribution Chart.
A copy of one of the charts used, showing how the experimental area was divided up into 30 2 x 2 metre-squares, each again divided into quarters. One prey was placed in each square and its position determined with playing cards (see text). The progress of male blackbird A across the grid is also shown.

DATE: 7th June 1983

TIME START: 2.37pm

WEATHER: Hot and sunny

TOTAL EATEN: 3W, 1WR, 3WG, 0G, 3GR, 0G = 10
(7 WHITE, 3 GREEN)



Each 4 metre square of the experimental grid was divided into four quarters and each quarter was assigned one of the four suits in a pack of playing cards. Playing cards were used to assign the positions of each prey type. Cards numbered from 1 - 6 (i.e. Ace = 1, etc.) of all four suits were used. The prey types were each assigned a card: **W** = 1; **WR** = 2; **WG** = 3; **G** = 4; **GR** = 5; **GG** = 6. The cards were shuffled thoroughly and then dealt out. The 4 metre squares were filled in order as follows: the first card gave the prey type and in which quarter of the first square it should be placed, i.e. the 4 of spades meant that a **G** prey should be placed in the top left quarter of the square; the next card was then dealt for the second square. (If it was a 4 again, for example, it would be ignored and the next card dealt.) The procedure was repeated until one of all six prey types had been distributed within a block. The cards were then reshuffled and dealt again for the next block. A specimen distribution chart is shown in Fig. 4.1. A number of different distribution charts were made. These charts were used when the experimental prey populations were put out in the grass grid. The prey distributions were changed daily or after five bouts of feeding to prevent the birds learning the positions of the prey.

The experimental populations were observed and species of birds seen feeding were recorded. When possible the paths of individual birds across the grid were sketched onto copies of the distribution chart.

Eaten prey were frequently replaced to ensure a constant ratio of the prey types, and the experiment was continued until 100 prey had been taken. If more than 15 prey had been eaten before replacement these results were excluded from the analysis.

There were two replicates in 1982 and four in 1983:
1982: August 12 - August 25
1983: June 7 - June 9

TABLE 4.2: Totals of each prey type taken in Experiment 2, Series 1, with results from G tests for Goodness of Fit to a 1:1:1:1:1:1 distribution within a replicate and for Heterogeneity between replicates within each background.

			TOTAL NUMBER OF EACH PREY TYPE TAKEN								
BACKGROUND	YEAR	REPLICATE	W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
Canvas	82	1	34	10	9	12	18	18	101	22,56	<0,001
Grass	82	1	38	22	28	7	7	4	106	55,24	<0,001
Canvas	82	2	28	21	24	10	8	10	101	21,82	<0,001
Grass	82	2	33	17	27	10	9	5	101	36,03	<0,001
Canvas	83	3	22	13	22	13	18	13	101	5,75	N,S,
Grass	83	3	25	11	28	8	15	12	99	19,16	<0,01
Canvas	83	4	31	17	24	12	14	11	109	15,79	<0,01
Grass	83	4	40	15	38	2	4	6	105	86,15	<0,001
CANVAS GRAND TOTAL			115	61	79	47	58	52	412		
GRASS GRAND TOTAL			136	65	121	27	35	27	411		

G tests for heterogeneity CANVAS; $G_{adj(15)}$ = 24,12 N,S,
GRASS; $G_{adj(15)}$ = 28,31 $p<0,05$

TABLE 4.3: Experiment 2, Series 1 - results of paired comparisons between corresponding canvas and grass replicates (G tests of independence).

YEAR	REPLICATES	$G_{adj(5)}$	p
1982	Canvas 1 v Grass 1	30.31	<0.001
	Canvas 2 v Grass 2	2.73	N.S.
1983	Canvas 3 v Grass 3	2.53	N.S.
	Canvas 4 v Grass 4	19.22	<0.01

4.3 RESULTS

4.3.1 Experiment 2: High Density - Series 1, Prey types: W WR WG G GR GG

The results are given in Table 4.2.

In the first canvas experiment, Canvas 1, the birds exhibited a highly statistically significant preference for the plain white prey type (**W**) over the other prey types. However, different species of birds appeared to prefer different prey background coloration. For example, of the ten prey seen to be taken by chaffinches, seven were green prey; whereas of the 31 taken by starlings, 22 were white. A woodpigeon was observed to take at least nine prey in a row and of these only one was white. Overall, approximately the same number of white prey (**W+WR+WG**) and green prey (**G+GR+GG**) were taken, but when the white prey were eaten they tended to be the plain prey type (**W**).

Fewer green prey (**G+GR+GG**) were eaten in the first grass experiment, Grass 1, than in Canvas 1. **W** was still the most heavily predated prey type but **WR** and **WG** suffered relatively more predation than before. **GG** was taken the least - only four times in a total of 106 prey eaten. This difference between the two experiments is highly statistically significant (Table 4.3). More species of bird had been observed feeding in the grass experiment than in the canvas experiment (Table 4.1). Two blackbirds fed for the first time and were seen to take 41 white prey types but no green prey types. This could have been due to the three white prey types being more conspicuous than the three green prey types or the blackbirds could have had a strong background-independent preference for the white prey types over the green. It was hoped that future replicates would yield more data on this point.

The second canvas replicate (Canvas 2) showed an increased preference for the white prey type over the green prey types, but within each prey colour group the three types were taken equally. There is a statistically significant difference in the proportions of the prey types eaten between Canvas 1 and Canvas 2 ($G_{adj(5)} = 17.75$, $p<0.01$).

The results from Grass 2 do not differ significantly from those of Canvas 2 (Table 4.3). There was a drop in the number of **GG** eaten - from ten out of a total of 101 prey eaten to five out of a total of 101, but this drop is not statistically significant.

The following year (1983), no statistically significant preferences for any of the six prey types were exhibited by the birds in Canvas 3. In Grass 3, statistically significantly more white prey types were eaten than green prey types. Fewer red-striped white prey (**WR**) were eaten than either of the other two white prey types. This result appears to be due to preferences of individual birds (Tables 4.4 and 4.5). One of the two male blackbirds (A) that were regular visitors to the experimental area, showed a strong aversion to the **WR** prey type. The second male blackbird (B) showed a strong preference for the white prey types: no green prey were taken by it. The overall result was that fewer green prey types were eaten in this grass replicate than in its preceding canvas replicate but the overall distributions of the prey types eaten did not differ significantly between replicates (Table 4.3).

The results from the second canvas replicate in 1983 (Canvas 4) reaffirmed the conclusion drawn from previous replicates that the birds had an overall preference for the white prey types over the green prey types, although this preference was not exhibited by all the birds, (for example, male blackbird B). The corresponding grass replicate (Grass 4) showed an increase in the proportion of white prey types taken and this was statistically significant (Table 4.3).

Two blackbirds had their predation recorded in detail in the 1983 replicates (Tables 4.4 and 4.5). Both were male blackbirds: A and B. A was a young blackbird and was the territory-holder for the area in which the experiments took place. B was an older blackbird that acted as an intruder and was chased off by A. A had a preference for the green prey types when presented with a choice between them and the white prey types in the canvas experiments; this preference was reversed in the grass experiments (Table 4.4). Blackbird B preferred the white prey types throughout the experiments (Table 4.5).

TABLE 4.4: Predation by male blackbird A in Experiment 2, Series 1. Table 4.4a refers to predation where all the prey types could be distinguished by the observer; Table 4.4b refers to predation where only the ground colour of the prey could be distinguished (and includes prey from Table 4.4a).

Table 4.4a

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
Canvas	3	1	2	4	2	5	2	16	-	-
Grass	3	8	1	7	4	7	5	32	7,81	N,S,
Canvas	4	2	2	6	3	6	4	23	-	-
Grass	4	31	6	31	2	3	6	79	70,91	<0,001
CANVAS GRAND TOTAL		3	4	10	7	5	11	39	7,85	N,S,
GRASS GRAND TOTAL		39	7	38	6	10	11	91		

<u>G test for heterogeneity</u> GRASS: $G_{adj(5)} = 15,60$ $p<0,01$

<u>Results from G tests for goodness of fit</u>:

GRASS 3 WHITE 1:1:1 $G_{adj(2)} = 6,67$ $p<0,05$
GREEN 1:1:1 $G_{adj(2)} = 0,83$ N,S,
WHITE:GREEN $G_{adj(1)} = 0,00$ N,S,
GRASS 4 WHITE 1:1:1 $G_{adj(2)} = 22,65$ $p<0,001$
GREEN 1:1:1 -
WHITE:GREEN $G_{adj(1)} = 45,46$ $p<0,001$

Table 4.4b

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY COLOUR TAKEN WHITE	GREEN	TOTAL	$G_{adj(1)}$	p
Canvas	3	8	12	20	0,81	N,S,
Grass	3	43	22	65	6,91	<0,01
Canvas	4	16	30	46	4,33	<0,05
Grass	4	68	10	78	48,39	<0,001
CANVAS GRAND TOTAL		24	42	68	4,94	<0,05
GRASS GRAND TOTAL		111	32	143		

<u>G tests for heterogeneity</u>:

CANVAS: $G_{adj(1)} = 0,16$ N,S,
GRASS: $G_{adj(1)} = 9,11$ $p<0,01$
Canvas 3 v Grass 3: $G_{adj(1)} = 4,17$ $p<0,05$
Canvas 4 v Grass 4: $G_{adj(1)} = 36,76$ $p<0,001$

TABLE 4.5: Predation by male blackbird B in Experiment 2, Series 1. Table 4.5a refers to predation where all the prey types could be distinguished by the observer; Table 4.5b refers to predation where only the ground colour of the prey could be distinguished (and includes prey from Table 4.5a).

Table 4,5a

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
Grass	3	0	2	4	0	0	0	10	-	-
Canvas	4	4	4	2	0	0	0	6	-	-
Grass	4	9	9	7	0	1	0	26	-	-
GRASS GRAND TOTAL		9	11	11	0	1	0	36	29,43	<0,001

Table 4,5b

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY COLOUR TAKEN WHITE	GREEN	TOTAL	$G_{adj(1)}$	p
Canvas	3	12	2	14	7,65	<0,01
Grass	3	10	0	10	13,20	<0,001
Canvas	4	30	0	30	52,00	<0,001
Grass	4	25	1	26	27,05	<0,001
CANVAS GRAND TOTAL		42	2	44	44,22	<0,001
GRASS GRAND TOTAL		35	1	36	40,21	<0,001

<u>G tests for heterogeneity:</u>
CANVAS; $G_{adj(1)}$ = 3,68 N,S,
GRASS; $G_{adj(1)}$ = 0,40 N,S,
CANVAS v GRASS; $G_{adj(1)}$ = 0,15 N,S,

TABLE 4.6: Totals of each prey type taken in Experiment 2, Series 2, with results from G tests for Goodness of Fit to a 1:1:1 distribution within a trial and for Heterogeneity between trials within each background.

BACKGROUND	YEAR	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN G	GR	GG	TOTAL	$G_{adj(2)}$	p
Canvas	82	1	35	34	37	106	0,13	N,S,
Grass	82	1	39	46	24	109	7,28	<0,05
Canvas	83	2	40	35	37	112	0,34	N,S,
Grass	83	2	24	38	17	79	8,47	<0,05
Canvas	83	3	33	29	38	100	1,21	N,S,
Grass	83	3	35	41	28	104	2,45	N,S,
	CANVAS GRAND TOTAL		108	98	112	318	0,99	N,S,
	GRASS GRAND TOTAL		98	125	69	292	16,37	<0,001

G tests for heterogeneity CANVAS; $G_{adj(4)}$ = 0,69 N,S,
GRASS; $G_{adj(4)}$ = 1,91 N,S,

TABLE 4.7: Experiment 2, Series 2 - results of paired comparisons between corresponding canvas and grass replicates (G tests of independence).

YEAR	REPLICATES	$G_{adj(2)}$	p
1982	Canvas 1 v Grass 1	4.73	<0.1
1983	Canvas 2 v Grass 2	5.96	<0.1
	Canvas 3 v Grass 3	3.57	N.S.

There was no overall heterogeneity between distributions in the four canvas replicates although there was heterogeneity between the two replicates in 1982 (Table 4.2). However, there was significant heterogeneity between the four grass replicates (Table 4.2).

4.3.2 Experiment 2: High Density - Series 2, Prey types: G GR GG

The results for this series are given in Table 4.6.

No statistically significant preferences for any of the three green prey types were found in any of the three canvas replicates.

In Grass 1, a statistically significant deviation from a 1:1:1 expected distribution of predated prey was observed, although the totals did not differ significantly from those observed in the corresponding canvas replicate, Canvas 1 (Table 4.7). **GR** was the most frequently taken prey type and **GG** the least.

The results from Grass 2 were not significantly different from those of Grass 1 ($G_{adj(2)}$ = 1.47): there was a statistically significant deviation from a 1:1:1 predation ratio. More **GR** and fewer **GG** were eaten than in the corresponding canvas trial (Canvas 2), although this result is not statistically significant (Table 4.7).

In the third grass replicate (Grass 3), no statistically significant preferences for any of the three prey types were found although, like the other two grass replicates, the **GR** prey were eaten more than the other two prey types and the **GG** prey were eaten the least.

There was no heterogeneity within canvas replicates or within grass replicates (Table 4.6) and therefore the totals were used to give a clearer picture of any selective predation. There was a significant difference in the proportions of the grand totals of the three green prey types eaten between the grass and the canvas experiments ($G_{adj(2)}$ = 12.925, $p<0.01$). In the grass replicates, significantly more **G** prey were eaten than **GG** ($G_{adj(1)}$ = 5.05, $p<0.05$) whereas there was no significant difference in the canvas replicates ($G_{adj(1)}$ = 0.07).

TABLE 4.8: Predation by male blackbird B in Experiment 2, Series 2.

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN			TOTAL	$G_{adj(2)}$	p
		G	GR	GG			
Canvas	2	17	14	13	44	0,57	N,S,
Grass	2	13	23	10	46	5,73	N,S,
Canvas	3	12	14	15	41	0,35	N,S,
Grass	3	16	18	9	43	3,29	N,S,
CANVAS GRAND TOTAL		29	28	28	85	0,02	N,S,
GRASS GRAND TOTAL		29	41	19	89	8,22	<0,02

<u>G tests for heterogeneity:</u>
CANVAS: $G_{adj(2)}$ = 0,88 N,S,
GRASS: $G_{adj(2)}$ = 0,87 N,S,
CANVAS v GRASS: $G_{adj(2)}$ = 4,06 N,S,

TABLE 4.9: Predation by female blackbird Y in Experiment 2, Series 2.

BACKGROUND	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN			TOTAL	$G_{adj(2)}$	p
		G	GR	GG			
Canvas	3	4	5	5	14	-	-
Grass	3	6	12	2	20	7,77	<0,05

The male blackbird A took very few prey during the course of this experiment. Individual data was obtained for male blackbird B and a new female blackbird, Y (Tables 4.8 and 4.9). Both these birds showed no preferences for any of the three prey types in the canvas replicates, but they had significant preferences for the **GR** prey type in the grass replicates (Tables 4.8 and 4.9). **GG** was taken the least by both birds in the grass replicates.

4.3.3 Experiment 2: High Density - Series 3, Prey types: W WR WG

The results for this series are shown in Table 4.10.

The results from Canvas 1a indicated no preferences for any of the three white prey types. After this first experiment was completed, there was a gap of over two weeks because of heavy rain and it was decided to repeat the canvas experiment before doing a grass experiment (see Section 4.2.4). The results of Canvas 1b were significantly different from those of the first replicate ($G_{adj(2)} = 9.07$, $p < 0.02$): relatively more **W** were taken and relatively fewer **WR**, but the number of **WG** taken was relatively similar. A young blackbird was seen feeding in this second canvas replicate, and this bird had not been seen previously in 1982. The prey were novel to this blackbird and perhaps, therefore, it was behaving in a similar way to the birds in the very first canvas replicate, in Series 1. (As the bird was not ringed, it could have been male A of 1983 - but there is no way of being certain.)

The first grass replicate, Grass 1, showed no statistically significant deviation from a 1:1:1 predation distribution (Table 4.10) and thus differed significantly from the results in Canvas 1b (Table 4.11).

Predation appeared random in Canvas 2 (Table 4.10). In Grass 2 fewer **WR** prey were eaten than either of the other prey types and this resulted in a significant deviation from a 1:1:1 distribution of predation (Table 4.10), but it did not differ significantly from the results of Canvas 2 (Table 4.11), probably because **WR** was also the least predated prey type in Canvas 2.

TABLE 4.10: Totals of each prey type taken in Experiment 2, Series 3, with results from G tests for Goodness of Fit to a 1:1:1 distribution within a replicate and for Heterogeneity between replicates within each background.

BACKGROUND	YEAR	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN W	WR	WG	TOTAL	$G_{adj(2)}$	p
Canvas	82	1a	38	30	32	100	1,02	N.S.
Canvas	82	1b	58	15	32	105	27,26	<0,001
Grass	82	1	37	26	39	102	2,99	N.S.
Canvas	83	2	44	25	38	107	5,49	<0,1
Grass	83	2	55	15	41	111	24,90	<0,001
Canvas	83	3	41	13	28	82	15,15	<0,001
Grass	83	3	44	18	29	91	11,34	<0,01
	CANVAS GRAND TOTAL		181	83	130	394	37,22	<0,001
	GRASS GRAND TOTAL		136	59	109	304	32,04	<0,001

G tests for heterogeneity: CANVAS; $G_{adj(6)} = 11,87$ $p<0,1$
GRASS; $G_{adj(4)} = 7,10$ N.S.
TOTAL CANVAS v TOTAL GRASS; $G_{adj(2)} = 0,69$ N.S.

TABLE 4.11: Experiment 2, Series 3 - results of paired comparisons between corresponding canvas and grass replicates (G tests of independence).

YEAR	REPLICATES	$G_{adj(2)}$	p
1982	Canvas 1b v Grass 1	8.23	<0.05
1983	Canvas 2 v Grass 2	3.79	N.S.
	Canvas 3 v Grass 3	0.47	N.S.

VR was eaten the least in both Canvas 3 and Grass 3, which resulted in significant deviations from 1:1:1 distributions (Table 4.10); and the results from the two replicates were very similar (Table 4.11).

In 1983 data were obtained from the two male blackbirds, **A** and B (Tables 4.12 and 4.13). Male B did not seem to show any consistent preferences, whereas male **A** tended to avoid **VR**, regardless of background.

There was no overall heterogeneity within the canvas replicates or within the grass replicates (Table 4.10). Background did not have any overall effect on predation by the birds (G test for Independence between grand totals of Canvas and Grass: $G_{adj(2)}$ = 0.69). However, there were significantly fewer **VG** prey eaten than **G** prey in the grass replicates ($G_{adj(1)}$ = 4.99, $p<0.05$) but a similar result was not found in the canvas experiment ($G_{adj(1)}$ = 2.39) although **VG** was eaten the least; this is probably a background-independent result.

Direct comparisons were made between Series 2 and 3 for the grand totals of prey eaten in the canvas replicates and in the grass replicates. G tests of independence showed that there were significant differences between the two series (Canvas: $G_{adj(2)}$ = 13.06, $p<0.01$; Grass: $G_{adj(2)}$ = 13.35, $p<0.01$). Therefore the three white prey types were selected in different proportions to the three green prey types on the same backgrounds; the only difference between the white and the green prey was the ground colour of the prey.

4.3.4 Experiment 3: Low Density

The results are given in Table 4.14.

The first and second replicates were carried out in 1982. In Replicate 1, there was no statistically significant deviation from a 1:1:1:1:1:1 distribution of prey eaten; however, more of the three white prey types were eaten in total than the three green prey types

TABLE 4.12: Predation by male blackbird A in Experiment 2, Series 3.

		TOTAL NUMBER OF EACH PREY TYPE TAKEN					
BACKGROUND	REPLICATE	**V**	**VR**	**VG**	TOTAL	$G_{adj(2)}$	p
Canvas	2	8	2	4	14	–	–
Grass	2	32	4	29	65	28.35	<0.001
Canvas	3	13	0	5	18	17.63	<0.001
Grass	3	23	0	6	29	33.38	<0.001
CANVAS GRAND TOTAL		21	2	9	32	18.32	<0.001
GRASS GRAND TOTAL		55	4	35	94	52.80	<0.001

G tests for heterogeneity:

GRASS: $G_{adj(2)} = 8.58$ $p<0.05$

TABLE 4.13: Predation by male blackbird B in Experiment 2, Series 3.

		TOTAL NUMBER OF EACH PREY TYPE TAKEN					
BACKGROUND	REPLICATE	**V**	**VR**	**VG**	TOTAL	$G_{adj(2)}$	p
Canvas	2	15	10	15	40	1.29	N.S.
Grass	2	4	3	4	11	–	–
Canvas	3	13	11	20	44	2.90	N.S.
Grass	3	4	7	9	20	2.00	N.S.

G tests for heterogeneity:

CANVAS: $G_{adj(2)} = 0.70$ N.S.

CANVAS v GRASS: $G_{adj(2)} = 0.83$ N.S.

TABLE 4.14: Totals of each prey type taken in Experiment 3, with results from G tests for Goodness of Fit to a 1:1:1:1:1:1 distribution within a replicate and for Heterogeneity within replicates.

		TOTAL NUMBER OF EACH PREY TYPE TAKEN								
YEAR	REPLICATE	W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
82	1	19	21	20	13	17	10	100	5,91	N.S.
82	2	15	13	11	6	15	10	70	5,45	N.S.
83	3	28	9	28	11	18	11	105	21,02	<0,001
83	4	31	27	25	12	4	6	105	42,52	<0,001
83	5	20	20	30	9	18	6	103	22,92	<0,001
83	6	23	16	19	11	17	11	97	6,71	N.S.
	TOTAL	136	106	133	62	89	54	580	64,48	<0,001

G test for heterogeneity: $G_{adj(25)} = 40,47$ $p<0,05$

($G_{adj(1)}$ = 4.01, $p<0.05$). In Replicate 2, there was an increase in the number of **GR** eaten but there was no heterogeneity between replicates.

Replicates 3, 4, 5 and 6 were carried out in 1983. There was heterogeneity between replicates ($G_{adj(15)}$ = 30.72, $p<0.01$). Comparison between individual replicates showed that this was due to the distribution of prey taken in Replicate 4 (G_{adj}s with 5 degrees of freedom: Replicates 3 v 4 = 20.49, $p<0.01$; Replicates 3 v 5 = 7.21, N.S.; Replicates 3 v 6 = 3.85, N.S.; Replicates 4 v 5 = 13.63, $p<0.02$; Replicates 4 v 6 = 14.42, $p<0.02$; Replicates 5 v 6 = 4.59, N.S.). This heterogeneity appeared to be the result of the three white prey types contributing to a relatively greater proportion of the total of prey eaten in Replicate 4 (Table 4.14). There were consistently more of the three white prey types taken than the three green prey types in these four replicates. **WR** was the least predated white prey type, and **GR** was the most heavily predated green prey type overall. **GG** seemed to be taken marginally less often than **G**.

There was no heterogeneity between the replicates from 1982 and Replicates 3, 5 and 6 ($G_{adj(5)}$ = 5.68, N.S.), therefore there was, on the whole, a consistent preference for certain prey types over others.

In 1983 results were obtained for two blackbirds: Male **A** and Female Y (Tables 4.15 and 4.16). For the male blackbird A, the numbers in three of the replicates were too small to allow detailed statistical analysis. However, the results did show that this blackbird continued to avoid **WR** (as it did previously in Experiment 2). Despite it avoiding the **WR** prey type, it took more white prey types in total than green prey types. The female blackbird Y also ate more white prey types than green prey types. It showed no preferences for any prey types within the two prey colour groups. There was significant heterogeneity between the distributions of the prey types eaten by these two blackbirds ($G_{adj(5)}$ = 20.99, $p<0.001$): this was due to the male's avoidance of **WR**.

TABLE 4.15: Predation by male blackbird A in Experiment 3.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN								
REPLICATE	W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
3	20	3	19	7	12	8	69	21,06	$<0,001$
4	3	1	3	1	1	0	9	-	-
5	1	1	3	0	1	0	6	-	-
6	4	0	4	2	2	2	14	-	-
TOTAL	28	5	29	10	16	10	98	30,99	$<0,001$

Results from G tests for goodness of fit:

WHITE 1:1:1 $G_{adj(2)} = 22,23$ $p<0,01$
GREEN 1:1:1 $G_{adj(2)} = 1,88$ N,S,
WHITE:GREEN $G_{adj(1)} = 6,95$ $p<0,01$

TABLE 4.16: Predation by female blackbird Y in Experiment 3.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN								
REPLICATE	W	WR	WG	G	GR	GG	TOTAL	$G_{adj(5)}$	p
3	8	5	7	4	7	3	34	3,46	N,S,
4	18	21	14	7	2	4	66	29,87	$<0,001$
5	1	3	3	3	2	0	11	-	-
6	4	6	3	3	5	2	23	-	-
TOTAL	31	35	27	16	16	9	134	24,11	$<0,001$

G test for heterogeneity:

REPLICATE 3 v REPLICATE 4 $G_{adj(5)} = 9,88$ $p<0,1$

Results from G tests for goodness of fit:

WHITE 1:1:1 $G_{adj(2)} = 1,03$ N,S,
GREEN 1:1:1 $G_{adj(2)} = 2,53$ N,S,
WHITE:GREEN $G_{adj(1)} = 20,64$ $p<0,001$

TABLE 4.17: Results of Mann-Whitney U-tests on the proportions of each prey type taken in the grass replicates of Experiment 2 compared with the replicates of Experiment 3.

PREY TYPE	p	Experiment with the greater proportion
W	$= 0.038$	2
WR	$= 0.476$	-
WG	$= 0.114$	-
G	$= 0.038$	3
GR	$= 0.090$	(3)
GG	$\geqslant 0.1$	-
Proportion of total white	$= 0.066$	2

4.3.5 Results from Experiment 2 compared with Experiment 3

There was a significant increase in the proportion of G prey types taken and a decrease in the proportion of **W** prey eaten at the lower density (Table 4.17).

4.4 DISCUSSION

These experiments demonstrated that, at two densities of 30 prey/m^2 and 1 prey/4m^2, garden birds preferred the prey types that were the most conspicuous (to the human eye) on a lawn background. The birds had an experiment-independent preference for the unmatching prey types, but this was increased when the prey were presented on grass. The colour of the stripe on four of the prey types had a significant influence on the preferences of the birds: the green stripe conferred an advantage on the matching prey type and the red stripe conferred a disadvantage. At the higher density of Experiment 2, the matching prey were eaten less than at the lower density of Experiment 3.

In Experiment 2, Series 1, there was a strong preference for the white prey types over the green prey types on both backgrounds, although this preference was not exhibited by all the birds. In spite of this preference for the white prey types, there was still a statistically significant difference in the proportion of the prey types taken on the two backgrounds. The inference is that the green prey types were less conspicuous than the white prey types on grass, and therefore they were more likely to be overlooked on grass by the feeding birds. There was heterogeneity between replicates on the grass backgrounds. There was a large increase in the preference for the white prey types over green prey types in replicate 4; and this can be seen clearly in the 1983 data for individual birds. The male blackbird A changed its preference from the green prey types in the canvas experiments to the white prey types in the grass experiments.

Male A showed a strong aversion to the **WR** prey type on both backgrounds and, since this bird was a major predator in 1983, the three white prey types were eaten in different proportions in both Series 1 and Series 3.

There were no consistent differences in the proportions of the three green prey types taken in Series 1; however, in Series 2, where there were no white prey types and therefore only a choice between the three green prey types there were consistent differences: in the grass replicates more **GR** prey and fewer **GG** prey were eaten than in the canvas replicates. This selective feeding was shown particularly well in the data for the male blackbird B (Table 4.8). These results indicated that the birds selected the prey on the basis of their colour patterns.

Series 3 showed that the proportions of the three white prey types eaten were not affected by the two backgrounds on which they were presented. **WR** was taken in much smaller numbers than were the other two prey types, due mainly to the preferences of the male blackbird A. This finding led to a further short series of experiments (see Chapter 5).

In Experiment 3, the overall trend was for the three white prey types to be more heavily predated than the three green prey types. As in Experiment 2, **WR** was the least predated of the white prey types and **GR** the most predated green prey type. **GG** was taken slightly less often than **G**. Fig. 4.1 gives an example of a sketch of the male blackbird A's progress across the grid. From following its movements it can be seen to walk quite close to a number of prey items without taking them.

In 1982 there were significantly different proportions of the six prey types eaten in Experiments 2, Series 1 when compared with Experiment 3. This could have been due to the change in the density of the prey population. It should be pointed out that different species of birds were involved in the two experiments - but no such difference occurred in 1983 and yet the experiments show the same trends. There was an increase in the proportion of **G** (and to some extent **GR**) prey taken at the lower density and a decrease in the proportion of **W** prey taken. This difference could have been because of the difference in experimental situation at the two densities. It might be predicted that predators would be more likely to overlook cryptic prey at low densities than at high densities (Tinbergen *et al.*, 1965). However, at a density of 30 prey/m^2 the birds were presented with a choice of prey without having to move very much between prey items. If it was relatively easier to find the white prey types it might have been more profitable to eat these first without spending the extra time needed to locate the green prey types. At the lower density, the birds had to actively search for the prey items. This searching might have put the green prey at a greater risk than in the higher density experiment where the birds had to choose between prey types.

Turner (1961) used cylindrical pastry prey of different colours and presented them on a lawn at a density of 24 prey per 100 square yards (approximately 1 prey/0.3m^2) to wild birds. In one of his experiments the birds were given a choice between prey that were either green, fawn, or green with a fawn dorsal stripe. He found that the striped prey was eaten significantly less than the plain prey. He attributed this result to the stripe acting disruptively on the prey. Another of Turner's experiments involved presenting the birds with a choice between white and green prey and found that more white prey were eaten than green. This result was interpreted as being caused by the white prey type being more conspicuous than the green prey type. One problem with analysing Turner's results is that he did no experiments to control for any pre-experimental preferences that his birds might have had for possible of the prey types; and so one cannot be sure that his results were not due to such experiment-independent preferences that the birds might have had. For example, my experiments showed that the birds had a strong preference for white pastry prey that was independent of the background.

Rake (1978) also gave garden birds a choice between striped and unstriped cylindrical pastry prey (7mm diameter, 7mm long) on grass lawns. The prey were presented at a density of 2 prey/m^2. She found that the striped prey were eaten less than the plain prey when the ground colour of the two types of prey were different, and this difference was in the same direction even if the ground colours of the two prey types was reversed. However, when the ground colour of the prey was the same there was no significant difference between the numbers of the two types eaten.

My results were therefore consistent with those of past experiments. All the three white prey types were at a greater risk from predation than any of the three green prey types on a grass background. The green prey with a green stripe was at the least risk from predation. This may have been due to it being better camouflaged than the other prey types on the stripy grass background. The red stripe of the **GR** prey did not represent a random sample of the background (*sensu* Endler, 1978) and therefore would not have acted to increase the crypsis of the green prey. These stripes could have acted disruptively if the birds searched specifically for oval prey: a disruptive pattern relies on breaking a familiar outline in such a way that the shapes that are seen are not recognised by the predator (Cott, 1940). The results from these experiments suggested that the green stripe probably was disruptive in that it broke the symmetrical shape of the oval prey. However, disruptive patterns are thought to be patterns of contrast that "catch the eye of the observer" and "draw his attention away from the shape which bears them" (Cott, 1940). The green stripe was made from dye that was a concentrated version of the prey ground colour, which resulted in this stripe being similar in colour to the background on which it was drawn, though it was appreciably darker. The red stripe presented a pattern that was in greater contrast to the green of the prey ground colour. Cott suggests that "the patterns themselves may be conspicuous enough, but since they contradict the form on which they are superimposed, they concentrate attention upon themselves" and that "by the contrast of some tones and the blending of others, certain portions of the object fade out completely while others stand out emphatically. And it is to be noted that the shape of the latter - which alone can be distinguished - is such that their real identity cannot be determined". Although the red stripe might have acted to draw the predator's attention away from the shape of the prey, it probably helped the birds to find the prey by being so conspicuous in itself. If the birds had been familiar only with the **G** prey type and were actively searching for this prey type, the red stripe may have acted to distract the birds from the other aspects of the prey and so prevent them recognising this prey type as prey. Familiarity with a particular shape is therefore important to the way a disruptive pattern 'works'. However, predators may prefer to feed on prey that they are familiar with, *per se*.

Experiments to examine this point were undertaken and are discussed in Chapters 6,7,8 and 9.

The use of the three-dimensional background of grass lawn and the design of the three green prey types proved to be successful and therefore they were used in further experiments (Chapters 6, 7 and 10).

4.5 SUMMARY

1. The aim of these experiments was to show whether wild birds prefer unmatching prey types, and whether the density at which the prey are presented affects this (or other) preferences for different prey types.
2. Garden birds were given a choice, at two densities, between pastry prey that varied in their ground colours and in their colour patterns.
3. The ground colours of the prey and the colour patterns used were so designed in order to ensure that the different prey either effectively matched or did not match the general impression of a lawn background.
4. The birds had a strong experiment-independent preference for the unmatching prey types, but it was shown that this preference was increased when the prey were presented on a lawn background.
5. The colour patterns of the prey had a significant influence on the outcome of the experiments, with the matching prey having an advantage conferred by the matching stripe but a disadvantage conferred by the conspicuous stripe.
6. The density at which the prey were presented also affected the outcome of the experiments. At the higher density, where the birds were presented with a choice between prey without having to move very much between prey items, the matching prey were eaten less than at the lower density, where the birds had to actively search between prey items. Possible reasons for this difference are discussed.
7. The use of grass lawn with these prey types has proved successful, resulting in grass lawns being used in many of my other experiments.

CHAPTER 5

EXPERIMENTS 6a, 6b, 6c & 6d - SOME EFFECTS OF PREY COLOUR ON THE FEEDING BEHAVIOUR OF INDIVIDUAL BLACKBIRDS

5.1 INTRODUCTION

This experiment arose out of some observations of individual blackbirds during Experiments 2 and 3 in the summer of 1983 (Chapter 4). It was noted that the male blackbird A almost totally avoided the red-striped white prey type (**WR**) and that this behaviour was not observed in the other blackbirds. However, this blackbird did not avoid the red-striped green prey type (**GR**). In order to try to find out what aspect of the prey caused such individual differences in behaviour, a short series of experiments was performed, using brightly coloured prey.

Each of the four experiments will be described in turn.

5.2 MATERIALS

5.2.1 Prey

Nine of the prey described in Chapter 2 were used in these experiments: plain white (**W**), red-striped white (**WR**), green-striped white (**WG**); red-coloured white (**R**) and dark red-striped white (**WDR**) (Plate 5.1); blue-coloured white (**B**) and blue-striped white (**WB**) (Plate 5.2); yellow-coloured white (**Y**) and yellow-striped white (**WY**) (Plate 5.3). **W**, **WR** and **WG** were the same prey types as used in Chapter 4, Plate 4.1.

5.2.2 Background

Most of the experiments were carried out on the same area of lawn as used in Experiment 2 at the Medical and Biological Sciences Building, Southampton University. Experiment 6d was repeated at another site: 10 Richmond Gardens, Highfield, Southampton (O.S. reference: SU 430145).

TABLE 5.1: Species of birds and individual blackbirds observed feeding in each experiment. The + sign indicates the presence of that species or individual. Scientific names are given in Table 2.1.

SITE	1																2		
EXPERIMENT	6a		6b				6c	6d											
								Red			Blue			Yellow			Red	Blue	Yellow
REPLICATE	1	2	1	2	3	4	1	1	2	3	1	2	3	1	2	3	1	2	3
Blackbird	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Starling	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-
Robin	-	-	+	-	+	-	-	+	+	+	+	+	+	+	+	+	-	-	-
Songthrush	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Collared dove	-	-	-	-	+	+	-	+	+	+	+	+	+	-	+	-	-	-	-
Chaffinch	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-
<u>Individual blackbirds</u>																			
Male A	+	+	+	+	+	+	+	+	+	-	+	+	+	+	-	-			
Male B	-	+	+	-	+	+	-	+	+	+	+	+	-	+	-	+			
Female Y	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+			
Male S																	+	+	+

5.2.3 Predators

Table 5.1 gives a list of the species of birds observed feeding and in which experiments.

5.3 EXPERIMENT 6a

5.3.1 Introduction

Since, in Experiment 2, Series 1, the male blackbird **A** only avoided the **WR** prey type and not the **GR** prey type, this experiment was designed to see if this avoidance was because of the contrast of red on white. If the bird had no preferences for any of the three prey types (**W, R, WG**), this would lend support to this reason. This experiment was the same as Experiment 2, Series 3 except that the **WR** prey type was replaced by the **R** prey type. The **R** prey type was a plain white prey that was painted red on the upper surface: thus the red 'stripe' covered the whole upper surface of the prey.

5.3.2 Prey Types

The prey types were plain white (**W**), red-coloured white (**R**) and green-striped white (**WG**).

5.3.3 Procedure

The procedure was as described in Chapter 4 for Experiment 2, Series 3. Thus the birds were given a choice between three prey types, ten of each, on a lawn background, at a density of 30 prey/m^2. Eaten prey were replaced until approximately 100 had been taken. There were two replicates, one per day over two days: 14th - 15th June 1983.

5.3.4 Results and Discussion

The results from this experiment are given in Table 5.2. The plain red prey type (**R**) was eaten significantly less than the other two prey types.

The male blackbird **A** was not observed eating any **R** prey at all (Table 5.3). Therefore it does not appear that this bird's original avoidance of **WR** was due to the contrast of a red stripe on a white

TABLE 5.2: Totals of each prey type taken in Experiment 6a, and G tests for Goodness of Fit to a 1:1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN					
REPLICATE	**W**	**R**	**VG**	TOTAL	$G_{adj(2)}$	p
1	51	9	37	97	33.21	<0.001
2	52	3	46	101	59.03	<0.001
TOTAL	103	12	83	198	88.52	<0.001

G test for heterogeneity: $G_{adj(2)} = 3.95$ N.S.

TABLE 5.3: Predation by male blackbird A in Experiment 6a, and G tests for Goodness of Fit to a 1:1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN					
REPLICATE	**W**	**R**	**VR**	TOTAL	$G_{adj(2)}$	p
1	13	0	10	23	18.51	<0.001
2	21	0	27	48	39.13	<0.001
TOTAL	34	0	37	71	57.15	<0.001

G test for heterogeneity $G_{adj(2)} = 1.005$ N.S.

background. There are two possible explanations for the results from this experiment. First, the bird had an innate 'dislike' for the red colour; this seems unlikely because the bird did not avoid red-striped prey on a green ground (**GR**) (Experiment 2, Series 1). Second, the avoidance behaviour was due, at least in part, to the novelty of the **R** prey type. To help determine a possible explanation, Experiment 6b was carried out.

5.4 EXPERIMENT 6b

5.4.1 Introduction

In this experiment, the birds were given a choice between the **VR** and **R** prey types, both of which had been avoided by the male blackbird A, in order to see which the birds preferred (or if they treated the two prey types equally). It was hoped that this experiment would show whether it was the colour red that the birds had avoided, which would result in both prey types being taken equally, or whether they would avoid the striped prey type (**VR**) or the prey with more of the red colour (**R**).

5.4.2 Prey Types

The prey types were the red-striped prey type (**VR**) and the plain red prey type (**R**) (see Section 5.4.1).

5.4.3 Procedure

The procedure was as for Experiment 6a but 15 of each of the two prey types were presented. Eaten prey were replaced until approximately 100 had been eaten (time permitting). There were four replicates over three days: 15th - 17th June 1983.

5.4.4 Results and Discussion

Table 5.4 gives the totals of each of the two prey types taken by all the birds overall. Consistently fewer **R** prey were taken in all four replicates, and in each case the departure from a 1:1 expectation was highly significant. There was no heterogeneity between replicates.

TABLE 5.4: Totals of each prey type taken in Experiment 6b, and G tests for Goodness of Fit to a 1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN				
REPLICATE	**WR**	**R**	TOTAL	$G_{adj(1)}$	p
1	76	23	99	29.76	<0.001
2	41	9	50	21.96	<0.001
3	76	22	98	31.32	<0.001
4	89	15	104	58.08	<0.001
TOTAL	282	69	351	138.46	<0.001

G test for heterogeneity: $G_{adj(3)} = 3.23$ N.S.

TABLE 5.5: Predation by male blackbird A in Experiment 6b, and G tests for Goodness of Fit to a 1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN				
REPLICATE	**WR**	**R**	TOTAL	$G_{adj(1)}$	p
1	20	3	23	13.77	<0.001
2	10	2	12	5.59	<0.02
3	4	0	4	-	-
4	30	0	30	40.91	<0.001
TOTAL	64	5	69	59.35	<0.001

G test for heterogeneity: $G_{adj(3)} = 5.56$ N.S.

TABLE 5.6: Predation by female blackbird Y in Experiment 6b, and G tests for Goodness of Fit to a 1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN				
REPLICATE	**VR**	**R**	TOTAL	$G_{adj(1)}$	p
1	22	3	25	15.99	<0.001
2	25	0	25	33.98	<0.001
3	48	1	49	57.58	<0.001
4	33	1	34	37.56	<0.001
TOTAL	128	5	133	141.23	<0.001

G test for heterogeneity: $G_{adj(3)}$ = 4.65 N.S.

TABLE 5.7: Predation by male blackbird B in Experiment 6b, and G tests for Goodness of Fit to a 1:1 distribution within replicates and for Heterogeneity between replicates.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN				
REPLICATE	**VR**	**R**	TOTAL	$G_{adj(1)}$	p
1	3	8	11	2.26	N.S.
2	-	-	-	-	-
3	4	13	17	4.87	<0.05
4	6	9	15	0.59	N.S.
TOTAL	13	30	43	6.91	<0.01

G test for heterogeneity: $G_{adj(2)}$ = 1.01 N.S.

Of the blackbirds observed feeding, Male A and Female Y avoided **R**, whereas Male B had a preference for **R** (Tables 5.5, 5.6 and 5.7). Male A's feeding behaviour was as expected if it had an aversion to the red colour - the **R** prey type had more red colour than the **WR** prey type. The results from Male A and from Female Y were not significantly different ($G_{adj(1)}$ = 1.06). Female Y did not have an aversion for the **WR** prey type in Experiment 3 (Table 4.16), and yet it showed an aversion for the **R** prey type in this experiment. This could have been due to the **R** prey type's novelty. On the other hand, Male B preferred the novel prey type. The results from Male B are significantly different from both Male A ($G_{adj(1)}$ = 49.67, $p<0.001$) and Female Y ($G_{adj(1)}$ = 78.53, $p<0.001$). These results suggest that there is much individual variation in behaviour among the birds. However, in evolutionary terms it is the overall selection that is important, and in this sense the **R** prey type was at a decided disadvantage (Table 5.4).

5.5 EXPERIMENT 6c

5.5.1 Introduction

Because of the method of application of the red colouring on the **R** prey type (see Chapter 2), the red colour was darker than that of the red stripe on the **WR** prey type. This meant that the red colours of the two prey types in Experiment 6b were different with respect to chroma (see Chapter 1, Section 1.1). The birds might have been choosing the prey type that had the palest red colour rather than choosing between striped and plain prey or between the prey with different amounts of the red colour. A new red-striped prey type was made that had a red stripe of the same colour as the red of the **R** prey type (**WDR**). In Experiment 6c, bird were given a choice between this prey type (**WDR**) and **WR** in order to see if the birds had any preferences for either prey type and if they had whether they were for the prey type with the paler red stripe (**WR**).

5.5.2 Prey Types

The prey were **WR** and **WDR** (see Section 5.5.1 above).

TABLE 5.8: Totals of each prey type taken in Experiment 6c, and G test for Goodness of Fit to a 1:1 distribution.

TOTAL NUMBER OF EACH PREY TYPE TAKEN				
VR	**VDR**	TOTAL	$G_{adj(1)}$	p
85	17	102	49.25	<0.001

5.5.3 Procedure

As in Experiment 6b. There was one replicate on the 20th June 1983.

5.5.4 Results and Discussion

The results are given in Table 5.8. Approximately 94% of the predation was by the male blackbird A. Significantly more **WR** prey were eaten than **WDR**. These results show that Male A could distinguish between these two red-striped prey types and that it had a strong preference for **WR**. This preference could have been due to either the novelty of the **WDR** prey type or an aversion to the darker red coloration.

5.6 EXPERIMENT 6d

5.6.1 Introduction

The theme of the previous experiments was extended in Experiment 6d. To test that the behaviour noted for Male A was not restricted to the colour red, two other colours were also used in this experiment. This possibility exists because the eyes of diurnal birds have efficient reception of red light (Verity, 1980). Many very different organisms use the colour red in signals to birds: these signals may attract (eg. in the form of flowers or fruit), or may repel (eg. in the form of dangerous or distasteful prey) (Cott, 1940).

Three sets of paired choice tests between white prey painted with one of the three colours (as for the **R** prey type) and white prey with a stripe of the same colour were given to birds at the same site as previously used in this series of experiments and at one other site.

5.6.2 Prey Types

The prey were plain-coloured red (**R**), dark red-striped white (**WDR**), plain-coloured blue (**B**), blue-striped white (**WB**), plain-coloured yellow (**Y**) and yellow-striped white (**WY**). (Plates 5.1, 5.2 and 5.3.)

PLATE 5.1: Experiment 6d. A 'population' of prey types **R** and **WDR** (with male blackbird A feeding).

PLATE 5.2: Experiment 6d. A 'population' of prey types **B** and **WB** (with male blackbird A feeding).

PLATE 5.3: Experiment 6d. A 'population' of prey types **Y** and **WY**.

5.6.3 Procedure

Equal numbers of plain and striped prey of the same colour were presented on grass in the manner described for Experiment 6b. As well as the experimental site used for Experiments 6a, 6b and 6c, a second site was used in this experiment to see if a different group of birds would respond to the different prey types in the way other birds were found to do at the first site.

In the experiment at Site 1, a random sequence with the one restraint that no colours followed twice (obtained from a 3 x 3 Latin Square) was used to obtain the order of presentation:

Site 1: RED, YELLOW, BLUE, YELLOW, BLUE, RED, BLUE, RED, YELLOW

Therefore there were three replicates per colour at Site 1. The experiment lasted over four days with two trials per day for the first three days and three trials on the fourth day. The experiment at Site 1 took place from 21st - 24th June 1983.

At Site 2, because of the slow rate of predation, there was one trial per colour with one colour per day over three days. Fewer prey were taken at this site, and trials were halted after approximately seven hours regardless of numbers of prey eaten. The experiment at Site 2 ran from 11th - 13th April 1984.

5.6.4 Results and Discussion

The results for each colour are given in Tables 5.9, 5.10 and 5.11. In all twelve replicates the striped prey type was eaten significantly more often than the plain prey type.

In the results from Site 1, there was heterogeneity within replicates in the Red and Blue series. In both these series the proportion of striped prey taken was highest in the first replicate and lowest in the third. In the Yellow series there was no heterogeneity within replicates, but again the striped prey were eaten in the lowest proportion in the third replicate. The decrease in each series of the proportion of striped prey taken with time could indicate that there was a waning in the birds' preferences for the striped prey types. The birds at Site 1 had encountered striped white prey before (in for example, Experiments 2, 3, 6a, 6b, 6c) and, although the colour of the

TABLE 5.9: Totals of each prey type taken in the Red replicates in Experiment 6d, and G tests for Goodness of fit to a 1:1 distribution within replicates and for Heterogeneity between replicates.

RED		TOTAL NUMBER OF EACH PREY TYPE TAKEN				
SITE	REPLICATE	**WDR**	**R**	TOTAL	$G_{adj(1)}$	p
1	1	89	11	100	68.98	<0.001
	2	78	26	104	27.08	<0.001
	3	59	24	83	15.14	<0.001
	TOTAL	226	61	287	100.76	<0.001
	<u>G test for heterogeneity</u>:				$G_{adj(2)}$ = 10.71	p<0.001
2	1	13	2	15	8.72	<0.01

TABLE 5.10: Totals of each prey type taken in the Blue replicates in Experiment 6d, and G tests for Goodness of Fit to to a 1:1 distribution within replicates and for Heterogeneity between replicates.

BLUE		TOTAL NUMBER OF EACH PREY TYPE TAKEN				
SITE	REPLICATE	**WB**	**B**	TOTAL	$G_{adj(1)}$	p
1	1	91	6	97	89.00	<0.001
	2	79	21	100	35.66	<0.001
	3	54	18	72	18.71	<0.001
	TOTAL	224	45	269	129.74	<0.001
	<u>G test for heterogeneity</u>:				$G_{adj(2)}$ = 13.94	p<0.001
2	1	12	0	12	15.97	<0.001

TABLE 5.11: Totals of each prey type taken in the Yellow replicates in Experiment 6d, and G tests for Goodness of Fit to a 1:1 distribueion within replicates and for Heterogeneity between replicates.

YELLOW		TOTAL NUMBER OF EACH PREY TYPE TAKEN				
SITE	REPLICATE	**WY**	**Y**	TOTAL	$G_{adj(1)}$	p
1	1	84	7	91	76.38	<0.001
	2	93	6	99	91.51	<0.001
	3	55	9	64	36.46	<0.001
	TOTAL	232	22	254	202.05	<0.001
	<u>G test for heterogeneity</u>:				$G_{adj(2)}$ = 2.97	N.S.
2	1	9	1	10	7.01	0.01

stripe may have been new (in the Blue and Yellow series), they therefore would have been more familiar with this type of striped prey. As blue and yellow were novel colours then the birds may have chosen that prey type in each series which presented them with the least amount of the 'new' colour - the striped blue and striped yellow types. An alternative explanation is that the birds had strong preferences for white prey and therefore chose the striped prey type because of their white ground colour.

Analysis of variance on the data from Site 1 (Tables 5.9, 5.10 and 5.11), showed that there was no significant difference between the results from the different colours ($F_{(2,6)} = 1.67$). The different colours in the trials did not appear to affect the birds' choices of striped and unstriped prey.

The pooled predation for each of the species and the predation by individual birds observed feeding at Site 1 showed the existence of preferences for the striped prey types over the plain ones (Tables 5.12 - 5.17). Even the male blackbird B, which had a preference for the **R** prey over **WR** in Experiment 6b (Table 5.7), showed a weak preference for the red-striped prey over the plain prey in this experiment (Table 5.12). There is no obvious explanation for this apparent change in behaviour but the data were too few to draw any clear inferences. The male blackbird A had very strong preferences for the striped prey types over the plain prey types (Table 5.13). The female blackbird Y also had clear preferences for the striped prey types although there was heterogeneity between replicates of the same colour (Table 5.14).

Predation was also observed by a single robin (recognisible by coloured rings), which took no **R** or **B** prey and only one **Y** prey (Table 5.15). Predation by collared doves (probably only one bird but this was impossible to verify) resulted in more of the striped prey types being eaten (Table 5.16), but this was not statistically significant. Predation by starlings also resulted in larger numbers of striped prey being taken but there is no evidence for any real preferences by these birds (Table 5.17).

TABLE 5.12: Totals of each prey type taken by male blackbird B at Site 1 in Experiment 6d, with G tests for Goodness of Fit to a 1:1 distribution within replicates.

COLOUR	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN		TOTAL	$G_{adj(1)}$	p
RED		**WDR**	**R**			
	1	3	3	6	–	–
	2	2	2	4	–	–
	3	5	2	7	–	–
	TOTAL	10	7	17	0.52	N.S.
BLUE		**WB**	**B**			
	1	5	0	5	–	–
	2	–	–	–	–	–
	3	4	2	6	–	–
	TOTAL	9	2	11	4.61	<0.05
YELLOW		**WY**	**Y**			
	1	1	2	3	–	–
	2	3	0	3	–	–
	3	–	–	–	–	–
	TOTAL	4	2	6	–	–

TABLE 5.13: Totals of each prey type taken by male blackbird A at Site 1 in Experiment 6d, with G tests for Goodness of Fit to a 1:1 distribution within replicates.

COLOUR	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN		TOTAL	$G_{adj(1)}$	p
RED		**WDR**	**R**			
	1	33	2	35	32.72	<0.001
	2	7	2	9	–	–
	3	–	–	–	–	–
	TOTAL	40	4	44	33.81	<0.001
BLUE		**WB**	**B**			
	1	15	2	17	10.93	<0.001
	2	–	–	–	–	–
	3	–	–	–	–	–
	TOTAL	15	2	17	10.93	<0.001
YELLOW		**WY**	**Y**			
	1	40	5	45	30.65	<0.001
	2	7	0	7	–	–
	3	5	2	7	–	–
	TOTAL	52	7	59	38.49	<0.001

TABLE 5.14: Totals of each prey type taken by female blackbird Y at Site 1 in Experiment 6d, with G tests for Goodness of Fit to a 1:1 distribution within replicates and for Heterogeneity between replicates and Analysis of Variance between Colours.

COLOUR	REPLICATE	TOTAL NUMBER OF EACH PREY TYPE TAKEN		TOTAL	$G_{adj(1)}$	p
RED		**WDR**	**R**			
	1	41	4	45	35.00	<0.001
	2	49	10	59	27.86	<0.001
	3	87	14	51	10.65	<0.001
BLUE		**WB**	**B**			
	1	38	1	39	44.20	<0.001
	2	49	10	59	27.86	<0.001
	3	30	6	36	17.23	<0.001
YELLOW		**WY**	**Y**			
	1	30	0	30	40.91	<0.001
	2	50	2	52	54.61	<0.001
	3	49	7	56	35.12	<0.001

G tests for heterogeneity between replicates:
Red: $G_{adj(2)} = 5.65$ $p<0.1$
Blue: $G_{adj(2)} = 6.24$ $p<0.05$
Yellow: $G_{adj(2)} = 6.83$ $p<0.05$

Analysis of Variance between Colours: $F_{(2,6)} = 1.86$ N.S.

TABLE 5.15: Totals of each prey type taken by a robin at Site 1 in Experiment 6d.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN					
	RED		BLUE		YELLOW	
REPLICATE	**WDR**	**R**	**WB**	**B**	**WY**	**Y**
1	1	0	5	0	2	0
2	5	0	3	0	1	1
3	2	0	5	0	1	0
TOTAL	8	0	13	0*	4	1

G test for Goodness of Fit to a 1:1 distribution:

* $G_{adj(1)} = 13.77$ $p<0.01$

TABLE 5.16: Totals of each prey type taken by collared doves at Site 1 in Experiment 6d.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN					
	RED		BLUE		YELLOW	
REPLICATE	**WDR**	**R**	**WB**	**B**	**WY**	**Y**
1	1	0	4	2	–	–
2	10	5*	0	1	2	0
3	–	–	–	–	–	–
TOTAL	11	5**	4	3	2	0

G test for Goodness of Fit to a 1:1 distribution:

* $G_{adj(1)} = 1.64$ N.S.

** $G_{adj(1)} = 2.24$ N.S.

TABLE 5.17: Totals of each prey type taken by starlings at Site 1 in Experiment 6d.

	TOTAL NUMBER OF EACH PREY TYPE TAKEN					
	RED		BLUE		YELLOW	
REPLICATE	**WDR**	**R**	**WB**	**B**	**WY**	**Y**
1	3	1	2	0	–	–
2	–	–	5	5	4	2
3	1	1	3	1	–	–
TOTAL	4	2	10	6*	4	2

G test for Goodness of Fit to a 1:1 distribution:

* $G_{adj(1)} = 0.98$ N.S.

In the trials at Site 2, the striped prey types were also eaten significantly more than the plain prey types (Tables 5.10, 5.11 and 5.12). All observed predation was by a single male blackbird (Male S) and it is probable that this bird was responsible for all predation. Starlings and sparrows were observed investigating the prey population at the start of the first trial (Yellow) but they did not touch the prey; it is possible that, since the prey were novel to the birds at this site, they did not recognise them as food. However, all six of the prey types were novel to the blackbird that did eventually feed at this site (nothing was eaten on the day when the prey population was first presented and so the experiment was attempted again the following day - prey were put out at 7.10 am GMT but it was not until 10.38 am that the blackbird took its first prey) and, therefore, the explanation, suggested above, that the bird was choosing the prey types that were the more familiar was not supported at this site. The second explanation, suggested above, that the birds preferred the striped prey because of these preys' white ground, colour, seemed more consistent with the results from this site and with the results from Experiment 2, Series 1, suggesting that birds had preferences for the white prey over other coloured prey. There was no heterogeneity between the three colours at this site ($G_{adj(2)}$ = 2.07).

However, regression analysis on the results from Site 1 (Table 5.18), for the proportion (arc-sin transformed) of striped prey taken against replicate number irrespective of trial colour, indicated that a high proportion of the variation was due to linear regression. This meant that there was a linear decrease in the proportion of the striped prey types taken as the experiment progressed, which supports the idea that the birds' aversion for the plain prey decreased with time. Novelty might therefore still have been an important factor in the birds' feeding behaviour.

This experiment provided further evidence for the ability of birds to distinguish between plain and striped prey and that the two prey types were selected differently. There was evidence that the preferences shown by the birds decreased with time and this indicated that novelty might have been one factor affecting the birds' behaviour. Another explanation, which is not incompatible with that of novelty, is that the

TABLE 5.18: Experiment 6d - ANOVA table for the proportion of striped prey taken against replicate number, and regression analysis.

SOURCE	d.f.	S.S.	M.S.	F	p
Among Replicates	2	204,573	102,287	2,86	N.S.
Linear Regression	1	200,450	200,450	5,60	<0,1
Deviation from Regression	1	4,123	4,123	0,115	N.S.
Within Replicates	6	214,621	35,770		
Total	8	419,194			

Regression Coefficient $b_{x.y} = -5,78$

Standard Error of the Regression Coefficient = 0,829

Significance of the Regression Coefficient $t_{s(7)} = -6,972$ $p<0,001$

birds had preferences either for prey with more white pastry showing or for prey with less of the coloured dye. This might have been due to any past experiences of the birds with white bread or other predominantly white food, or because the birds associated the colours red, yellow and blue with distasteful or dangerous prey, and therefore initially avoided prey with more of these colours.

5.7 DISCUSSION

These four experiments examined the predation by a group of wild birds presented with artificial prey that were either plain or striped with bright conspicuous colours.

Experiment 6a gave the birds a choice between three prey types: plain white (**W**), plain white painted red on the upper surface (**R**), and green-striped white (**WG**). The birds ate very few of the **R** prey type, and some birds were observed eating none of this prey type. Possible explanations for this behaviour are: that the birds 'disliked' the colour red and/or that this result was due to the novelty of the **R** prey type whereas the birds were familiar from previous experiments (Chapter 4) with the other two prey types; or that the birds preferred prey with more of the white pastry visible, perhaps because this colour, with regard to prey or food, was more familiar.

Fear responses were noted in my experiments (casual observations only): starlings in particular, when confronted with the food for the first time, would peck at the **R** prey type and then jump backwards or even fly off before returning to carry off the prey; or the starlings would carry the **R** prey off rather than staying on the site to feed. Similar behaviour was observed in Experiments 6b and 6d. The starlings did not actually avoid the **R** prey type in Experiment 6a: they were known to have eaten most of the **R** prey that were taken in the two replicates (only 12 **R** prey eaten out of a total of 198) but, since they were feeding at the same time as a blackbird, it was impossible to record exactly what they were taking and therefore to know whether or not they had any preferences.

A predator's ability to respond to a stimulus depends on its level of arousal in neurological terms, and it is possible that some stimuli could increase the rate of attack by making the predator more alert, (and therefore behaviourally more efficient), or decrease the attack rate by 'overarousing' the animal (Coppinger, 1970). This second response was possibly what was observed in the starlings' behaviour since in other experiments (for example, in Experiment 2) their predation was much more intense and consistent. The starlings may have been stimulated by the bright red colour to attack the **R** prey type but they may have been overaroused by the colour and this caused inefficient predation behaviour.

It was possible that the birds were avoiding the colour red, perhaps because they were generalising experiences with red-coloured aposmatic prey. Bowers, Brown and Wheye (1985) conducted a survey on a population of the checkerspot butterfly, *Euphydryas chalcedona*, and collected the wings of eaten butterflies. They found differential predation on the population, apparently based on wing coloration. This butterfly species has extremely variable wing coloration and it was found that birds preferred butterflies with less red on the dorsal surface of the forewing: the females and the less red males. It could be inferred from this that the birds were avoiding the colour red, but, equally, they could have been choosing males that were more like the females (black and cream). Female *E. chalcedona* may provide a more optimal diet since they are larger than males and have additional fat.

Experiment 6b gave the birds the choice between the plain red prey type (**R**) from Experiment 6a and the red-striped prey type (**WR**) from Experiments 2 and 3. The birds had been shown to avoid both of these prey types. If familiarity had been a factor contributing to these results then one would have expected that the **R** prey type would have been preferred by the birds since this was the prey type that they had had the most recent experience with. But this was not the result. The birds in general avoided the **R** prey type (Table 5.4) except for the male blackbird B, which had a significant preference for the **R** prey type (Table 5.7).

Male B might have been showing a preference for a familiar prey type, but this bird was only observed feeding in the second replicate of Experiment 6a and ate eleven prey at most, of which only three could have been the **R** prey type. It had much more experience with the **VR** prey type from Experiments 2 and 3, and had shown no aversion to this prey type (see Chapter 4, Tables 4.5 and 4.15). In Experiment 6d, this bird took fewer of the plain-coloured prey types than the striped prey types, although the total numbers taken were too small for any firm conclusions to be drawn (Table 5.15). Therefore the most likely reason for the behaviour shown by Male B in Experiment 6b is that, although its experience with the **R** prey type was relatively small, it preferred the prey type with which it had had the most recent experience (**R**).

The other birds showed consistent preferences for the **VR** prey type. The possible explanations for these results are that the birds had a preference for the **VR** prey type that was not related to previous experience with the two prey types, that they had had more experience with the **VR** prey type and therefore preferred it, or that their behaviour was a result of a combination of these two influences.

The third experiment (6c) was carried out as a result of the observation that the red stripe on the **VR** prey type was not of the same intensity of red as that painted on the **R** prey type. This difference in colour resulted from the different methods of application (see Chapter 2, Section 2.3). It was therefore decided to test the preferences of the birds when they were given an equal choice between two red-striped prey differing in the intensity of the red colour. A new prey type (**VDR**) was made that had its red stripe of the same intensity of red colour as that of the **R** prey type, and the birds were presented with a prey population consisting of this prey type and the **VR** prey type. Almost all the predation was by the male blackbird A and there was a highly significant preference for the **VR** prey type. This could have been due to the **VDR** prey type being novel or to this blackbird having an aversion to red (or bright) coloration.

Experiment 6d was more complex than the previous experiments in this series. It compared striped and plain prey of three colours: red, blue and yellow. It was designed to answer the following questions. Do the birds only avoid the red colour? Do they behave differently toward the three colours? When both the striped and plain prey are equally new to the birds do they still show a preference for the striped prey type?

The results from this experiment were consistent with those from the three previous experiments. In all the trials the striped prey were eaten significantly more than the plain prey. There was a change in this preference with time: there was a decrease in the proportion of the striped prey taken as the experiment progressed. If the striped prey had more features in common with the birds' previous experiences, then Coppinger's (1969, 1970) proposal that the inhibition of attack is partly due to the amount of stimulus change fitted the observed responses.

If the birds associated the colours red and yellow with unpalatability, this would explain the preferences for the prey types that had less of these colours. It is unlikely that they had encountered prey coloured blue to any real extent in the wild, but they might have associated it with the 'metallic' colours that are found in many distasteful species of insects (Poulton, 1890; Morton Jones 1932, 1934; Cott, 1940). The colours used in Experiment 6d were three of the colours most commonly associated with aposematic coloration (Cott, 1940). Morton Jones (1932, 1934) conducted many experiments to determine the relative acceptability of some insects to insectivorous birds. He used wild birds and presented them with dead insects. In 1932 he found that, classifying the insects by coloration, 81% of the insects having a low acceptability rating exhibited one or other of two types of coloration: conspicuously patterned in yellow, orange or red, or brilliantly metallic in coloration; and not one of the ninety species and 2409 insects of those fully acceptable to the birds conformed to either of these types of coloration in its resting attitude.

Birds have been shown to avoid novel prey (Coppinger, 1969, 1970; Rabinowitch, 1965, 1968; Hogan, 1965) and birds may have been avoiding the **R** prey type in Experiment 6a for this reason. It has also been shown in many experiments that birds tend to eat proportionately more familiar than unfamiliar prey when given a choice (Allen and Clarke, 1968; Allen, 1974; Croze, 1970). The birds in Experiments 6b, 6c and 6d might have chosen the prey types with which they had more experience or prey types that were more generally familiar. Further experiments were performed to test whether birds preferred the familiar of striped or unstriped prey (Chapters 6 and 9) and whether they preferred prey that were the most similar to familiar prey (Chapters 7 and 8).

The experiments described in this Chapter further demonstrate that predation by various species and individuals of garden birds can be affected by their prey coloration including colour patterns. They also indicate that novelty and familiarity were factors contributing to the results.

5.8 SUMMARY

1. Garden birds were used in a series of four experiments in which they were presented with artificial prey that were conspicuously coloured. It had been observed in previous experiments (Chapter 4) that some birds, in particular a male blackbird (A), avoided eating a prey type that was white with a red stripe, and it was hoped that, by doing this series of experiments, it could be discovered whether this behaviour was due to the contrast of a red stripe on a white background or to the colour red *per se*.
2. Most of the experiments were carried out on the same site and at the same prey density (30 prey/m^2) as in Experiment 2, Chapter 4. Experiment 6d was repeated at another site to test whether the behaviour observed at the first site was common to other birds.
3. Experiment 6a replaced the **WR** prey type of Experiment 2, Series 3, which had been avoided by some of the birds, with a white prey type that had its upper surface painted red (**R**). Very few of this new prey type was eaten. The possibility that this result was due to novelty is discussed.
4. Experiment 6b gave the birds a choice between this **R** prey type and the red-striped white prey type (**WR**). The birds in general avoided the **R** prey type. Possible explanations for this result are that the birds had a preference for the **WR** prey type unrelated to their previous experiences with either prey type, that they had had more experience

with the **VR** prey type and preferred it for that reason, or that the outcome was a combination of these two factors.

5. Experiment 6c was carried out because the red colours in the two prey types used in Experiment 6b (**VR** and **R**) were not of the same intensities. Therefore the birds were given a choice between **VR** and a prey type that had its red stripe of the same intensity as that of **R**: **VDR**. Almost all the predation was by one blackbird which showed a highly significant preference for the **VR** prey type. This result could have been due to either the **VDR** prey type's novelty or to this blackbird having an aversion to red (or to bright) coloration.

6. Experiment 6d compared striped and plain prey of three colours: red, blue and yellow. It was hoped to discover whether the birds only avoided the colour red, if the birds behaved differently toward the three colours, and if they preferred the striped prey types even when both the striped and plain prey types were equally novel. The results were consistent with those from the previous experiments. In all the trials the striped prey were eaten significantly more than the plain prey. There was a decrease in the proportion of the striped prey taken as the experiment progressed. This change is consistent with the hypothesis that the birds were responding to the common features of their prey; and this is discussed.

7. Prey novelty and familiarity were probably important factors in determining the choices of the birds. Further experiments were undertaken with respect to familiarity.

8. Associations that the birds may have had between the various colours and unpalatability are discussed.

CHAPTER 6

EXPERIMENTS 5a, 5b & 5c: TRAINING EXPERIMENTS ON STRIPED AND UNSTRIPED ARTIFICIAL PREY - Do wild birds prefer the familiar of striped and unstriped prey?

6.1 INTRODUCTION

Disproportionate overpredation of common morphs (or 'apostatic selection', Clarke, 1962) is a mechanism that is capable of maintaining colour polymorphism in prey species. Evidence has been collected in support of this hypothesis (see Clarke, 1979; Greenwood, 1984 for recent reviews) but in all these studies the prey differed in **colour** alone. Yet in many polymorphic species some (or all) of the morphs are distinguished by **patterns** of pigments (stripes, blotches, dots, etc.) overlying a ground colour (See Chapter 1 this thesis; Ford, 1975; Endler, 1978). Experiments 5a, 5b and 5c were designed to test whether wild birds can feed in a manner that might lead to frequency-dependent selection on prey that differ only in the presence or absence of a coloured stripe. The results from Experiment 5a have been published (Raymond, 1984 - see General Appendix B).

The experiments were similar in design to those of Allen and Clarke (1968) and Allen (1974, 1984) in that wild birds were trained to search for artificial prey of one type and were then offered a choice between equal numbers of the familiar type and a second type. A preference of the birds for the familiar type can be interpreted as support for the hypothesis of apostatic selection. In nature, through chance encounter, predators are more likely to acquire preferences for prey types that are common and thus they will overlook rare (unfamiliar) forms. Previous training experiments have used prey types that differed in colour (Allen and Clarke, 1968; Allen, 1974, 1984; Croze, 1970; Harvey, Birley and Blackstock, 1975), shape (Croze, 1970) or size (Harvey *et al.*, 1975), but none have used prey that differed only in their colour patterns.

Experiment 5a used plain green (**G**) and red-striped green (**GR**) prey types. These two prey types were clearly distinct from each other and birds have been shown in Experiments 2 and 3 (Chapter 4) to be able to distinguish between these two prey types.

After the results from Experiment 5a were obtained (which showed that the birds preferred the familiar prey type), Experiment 5b was designed with prey types that were even more similar to each other. The same plain green prey type was used (**G**) but the green-striped green prey type (**GG**) was substituted for **GR**. The lengths of the training period and of the presentation of the 1:1 populations were shortened. These two changes in experimental design resulted in an experiment that was an extreme version of Experiment 5a, with very similar prey types and an extremely short training period (one day). If a similar training bias to that shown in Experiment 5a could have been obtained then this would have lent great weight to the conclusions already drawn from Experiment 5a and the experimental technique would have proved to be a highly practicable one.

Experiment 5b was partially successful, but the numbers of prey taken in the experiments were low. Because of this, Experiment 5c was performed using the design of Experiment 5a, with its longer training period, and the two very similar prey types from Experiment 5b.

6.2 MATERIALS AND METHODS

6.2.1 Prey

The prey were three of the prey types described in Chapter 2: plain green (G), green with a red stripe (**GR**) and green with a green stripe (**GG**). Experiment 5a used **G** and **GR** prey, and Experiments 5b and 5c used **G** and **GG** prey. (Plate 4.1, Chapter 4.)

6.2.2 Backgrounds and Sites

The prey populations were presented on grass lawns at six different sites in Experiment 5a, at two sites in Experiment 5b, and at two sites in Experiment 5c. Table 6.1 gives the Ordnance Survey map

TABLE 6.1: Sites, map references and chronology for Experiments 5a, 5b and 5c.

EXPERIMENT	SITE	ADDRESS	O.S. MAP REF.	CHRONOLOGY
5a	1	Boldrewood, Southampton University	SU 418156	28 Jan - 11 Feb 1983
	2	10 Richmond Gardens, Southampton	SU 430145	9 Feb - 23 Feb 1983
	3	Abbots Way, Southampton	SU 426145	11 Feb - 25 Feb 1983
	4	6 Oakhurst Road, Southampton	SU 422151	25 Feb - 11 Mar 1983
	5	9 Blenheim Avenue, Southampton	SU 421142	26 Mar - 23 Apr 1983
	6	25 Alma Road, Bristol	ST 575739	7 Apr - 21 Apr 1983
5b	1a	Boldrewood, Southampton University	SU 418156	27 Jun - 30 Jun 1983
	1b	" " "	"	11 Jul - 14 Jul 1983
	2a	Chamberlain Hall, Southampton	SU 421159	27 Jun - 30 Jun 1983
	2b	" " "	"	19 Jul - 23 Jul 1983
5c	1	10 Richmond Gardens, Southampton	SU 430145	7 Mar - 21 Mar 1983
	2	14 Portswood Park, Southampton	SU 426137	9 Mar - 23 Mar 1984

TABLE 6.2: Experiments 5a, 5b and 5c - species of birds observed feeding at each site. For scientific names see Table 2.1.

EXPERIMENT	5a						5b				5c	
SITE	1	2	3	4	5	6	1a	1b	2a	2b	1	2
Blackbird	+	+	–	+	+	+	+	+	+	+	+	+
Robin	+	–	–	–	–	+	+	+	–	–	+	–
House sparrow	–	+	–	–	–	+	–	–	–	–	+	–
Song thrush	–	–	–	–	+	–	–	–	–	–	–	+
Starling	–	–	–	–	–	–	+	–	–	–	+	–
Woodpigeon	+	–	–	–	–	–	–	–	–	–	–	–
Chaffinch	–	–	–	–	–	+	–	–	–	–	–	–
Magpie	–	–	+	–	–	–	–	–	–	–	–	–
Jay	–	–	–	–	–	–	–	–	–	+	–	–
Greenfinch	–	–	–	–	–	–	–	–	–	–	+	–

references for each site and the chronology of the experiments. Sites in Experiment 5a (Sites 1 - 5) were in Southampton and were separated by a minimum distance of 500m. The sixth site was in Bristol. The sites in Experiments 5b and 5c were approximately 650m and 900m apart respectively. Each experimental area was a rectangle marked out into metre-squares with metal tent pegs. The size of the plot (and therefore the size of the prey population) depended on the area of grass available, with a maximum experimental area of 10m x 5m and a minimum of 3m x 4m.

6.2.3 Predators

Table 6.2 lists the species of birds observed feeding at each site.

6.2.4 Procedure

Training consisted of scattering prey of one type over the experimental area for a period of five days in Experiments 5a and 5c, and for a period of one day for Experiment 5b. Between 300 and 1000 prey were eaten at each site in Experiment 5a, about 300 prey were eaten at each site in Experiment 5b, and between 230 and 600 prey were eaten in Experiment 5c. Experimental populations containing equal numbers of the two prey types were then presented for three days in Experiments 5a and 5c, and for two hours in Experiment 5b. These populations were at a density of 2 prey/m^2 and the prey were randomly distributed in Experiments 5a and 5b following a method similar to that used by Allen (1974). The four quarters of each metre-square were each assigned a suit from a pack of playing cards. Each prey type was assigned half the cards (Kings were discarded). The cards were thoroughly shuffled and then two cards dealt out one at a time to represent the positions of the two prey in a metre-square. These two prey were never positioned within the same quarter: this resulted in the rejection of any card that followed one designating the same quarter. The cards were then placed back in the pack, shuffled, and the procedure was then repeated until the positions of all the prey had been chosen. The positions were copied onto grids. From previous experiments it had been noted that experimental areas were not searched uniformly by the birds and therefore the areas were divided into sub-areas of 4-6 metre-squares that were allotted equal proportions of the two prey types. This ensured that there were no large differences in the frequencies of the two prey types between different areas of the population.

This method was time consuming and therefore a computer program was devised for Experiment 5c and other experiments that randomised the distributions of the prey populations and also printed them out. (See General Appendix A)

The prey were placed at random in their allocated quarter by dropping them from waist height and then adjusting them if necessary so that were level with their colour pattern uppermost.

To ensure that the birds did not learn the positions of the prey, the distributions were changed at least daily. The populations were maintained by repeated replacement of eaten prey and the numbers of each prey type taken were recorded at these times. The experimental populations were observed when practicable (the proportion of the predation that was observed was 91% in Experiment 5a, 100% in Experiment 5b and 65% in Experiment 5c) and, where possible, individual sets of data were collected for each species of bird.

The experiment was then repeated at each site but with the birds being trained on the prey type not used for the first training. At half the sites in Experiments 5a and 5c the birds were trained first on striped and at the other sites they were trained first on plain. At one site in Experiment 5b the birds were trained on striped and at the other site they were trained first on plain; this experiment was repeated in the reverse order after a period of one week. Therefore, in total, there were twelve experiments carried out in Experiment 5a, eight experiments in Experiment 5b and four in Experiment 5c.

TABLE 6.3: Experiment 5a - numbers of G and GR prey eaten from 1:1 populations after training, with values of G_{adj} for a departure from a 1:1 expectation and for independence of the two experiments at each site.

	TRAINED ON G		$G_{adj(1)}$		TRAINED ON GR		$G_{adj(1)}$	$G_{adj(1)}$
	Numbers taken		(deviation		Numbers taken		(deviation	(2 x 2,
SITE	G	GR	from 1:1)		G	GR	from 1:1)	heterogeneity)
1	92	78	1,15	→	105	145	6,43*	5,95*
2	146	114	3,95*	→	115	150	4,64*	8,54**
3	42	33	1,08	→	9	19	3,65	4,63*
4	34	23	2,14	←	12	29	7,27**	8,89**
5	5	8	0,70	←	10	18	2,32	0,03
6	156	141	0,76	←	82	31	11,37***	9,83**

Arrows indicate order of experiment. Asterisks indicate level of statistical significance; *p<0,05, **p<0,01, ***p<0,001.

TABLE 6.4: Experiment 5a - numbers of G and GR prey eaten by individual species of birds with values of G_{adj}

	SPECIES (estimated	TRAINED ON G		$G_{adj(1)}$		TRAINED ON GR		$G_{adj(1)}$	
	numbers of birds	Numbers taken		(deviation		Numbers taken		(deviation	$G_{adj(1)}$
SITE	in parenthesis)	G	GR	from 1:1)		G	GR	from 1:1)	(2 x 2)
1	Blackbird (1)	10	6	0,98	→	9	20	4,21*	4,04*
1	Robin (2)	18	11	1,68	→	6	24	11,38***	10,92***
1	Woodpigeon (2)	56	57	0,01	→	76	90	3,27	0,38
2	Sparrow (20+)	146	114	3,95*	→	115	146	3,68	7,62**
3	Magpie (2?)	6	6	0,00	→	9	14	1,07	0,36
4	Blackbird (4)	23	14	2,18	←	9	22	5,54*	7,43**
6	Sparrow (15+)	80	75	0,16	←	62	98	8,14**	5,25*

Arrows indicate order of experiment. Asterisks indicate level of statistical significance; *p<0,05, **p<0,01, ***p<0,001.

6.3 RESULTS

6.3.1 Experiment 5a

Table 6.3 gives the numbers of **G** and **GR** prey eaten during the presentations of the twelve 1:1 populations. There was no significant heterogeneity between the days of each experiment, except at Site 1 (**GR**-trained) where more familiar than unfamiliar prey were taken during the first two days and more unfamiliar than familiar prey were taken on the first day ($G_{adj(2)}$ = 10.22, $p<0.01$). In four of the **GR**-trained experiments and in one of the **G**-trained experiments there were statistically significant deviations from an expected 1:1 ratio, with the familiar form being overpredated. If the data are treated as twelve independent experiments, then in eleven out of twelve more of the familiar prey type were taken (p = 0.003, sign test). There was one exception but it involved very little predation. At five out of the six sites, the proportions of the two prey types taken differed significantly between the **G**-trained and **GR**-trained experiments (2 x 2 G tests); and, again, the site which did not show significant differences between experiments was the one where predation was low.

There was no statistically significant heterogeneity between sites when the birds were **G**-trained ($G_{adj(5)}$ = 2.76) or when they were **GR**-trained ($G_{adj(5)}$ = 4.78). Pooling the data again showed that significantly more of the familiar prey type were eaten after training (**G**-trained: $G_{adj(1)}$ = 6.98, $p<0.01$; **GR**-trained: $G_{adj(1)}$ = 30.82, $p<0.001$) and that, overall, the proportions of the two prey types taken in the two sorts of experiments differed significantly from one another ($G_{adj(1)}$ = 33.93, $p<0.001$). A comparison of the strength of the training response showed that a significantly higher proportion of **GR** was eaten in the **GR**-trained experiments than **G** in the **G**-trained experiments ($p<0.05$, Wilcoxon matched-pairs signed-ranks test).

Table 6.4 shows the observed data from Table 6.3 broken down into predation by species. Some individual species showed a clear response to training. Both groups of blackbirds, both groups of sparrows, and the single group of robins took significantly different proportions of the two prey types in the two experiments. There was no significant

TABLE 6.5: Experiment 5b - numbers of G and GG prey eaten from 1:1 populations after training, with values of G_{adj} for a departure from a 1:1 expectation and for independence of the two experiments at each site.

SITE	TRAINED ON G Numbers taken G	GG	$G_{adj(1)}$ (deviation from 1:1)		TRAINED ON GG Numbers taken G	GG	$G_{adj(1)}$ (deviation from 1:1)	$G_{adj(1)}$ (2 x 2, heterogeneity)
1a	43	40	0,11	←	55	73	2,53	1,57
1b	6	2	-	→	4	6	0,38	2,09
2a	13	10	0,38	→	13	21	1,87	1,80
2b	5	5	0,00	←	6	9	0,60	0,84

Arrows indicate order of experiment.

TABLE 6.6: Experiment 5b - total numbers of G and GG prey eaten from 1:1 populations after training, with values of G_{adj} for a departure from a 1:1 expectation and for independence of the two experiments.

	Numbers taken G	GG	TOTAL	$G_{adj(1)}$ from 1:1	p
G-TRAINED	67	57	124	0,80	N.S.
GG-TRAINED	78	109	187	5,15	$<0,05$
G test (2 x 2);	$G_{adj(1)} = 4,53$		$p<0,05$		

TABLE 6.7: Experiment 5b - numbers of G and GG prey eaten by individual species of birds with values of G_{adj}.

SITE	SPECIES (estimated numbers of birds in parenthesis)		TRAINED ON G Numbers taken G	GG	$G_{adj(1)}$ (deviation from 1:1)		TRAINED ON GG Numbers taken G	GG	$G_{adj(1)}$ (deviation from 1:1)	$G_{adj(1)}$ (2 x 2)
1a	Blackbird	(1)	26	20	0,78	←	29	39	1,47	2,09
1a	Robin	(1)	6	6	0,00	←	5	11	2,24	0,95
2a	Blackbird	(2)	13	10	0,38	→	13	21	1,87	1,80

Arrows indicate order of experiment.

heterogeneity between all seven groups of birds (**G**-trained: $G_{adj(6)}$ = 3.92; **GR**-trained: $G_{adj(6)}$ = 10.57). In twelve out of the fourteen sets of data given in Table 6.4 more of the familiar prey type was eaten ($p = 0.002$, sign test). Analysis on these data again showed that a higher proportion of **GR** was taken in the **GR**-trained experiments than **G** in the **G**-trained experiments ($p<0.05$, Wilcoxon matched-pairs signed-ranks test).

6.3.2 Experiment 5b

Table 6.5 gives the numbers of **G** and **GG** prey eaten during the presentations of the eight 1:1 populations. In seven out of eight experiments, more of the familiar prey type were taken after training ($p = 0.016$, sign test). There was no significant heterogeneity between experiments in each site (Site 1: **G**-trained: $G_{adj(1)}$ = 1.56; **GR**-trained: $G_{adj(1)}$ = 0.03; Site 2: **G**-trained: $G_{adj(1)}$ = 0.11; **GR**-trained: $G_{adj(1)}$ = 0.01) or between sites (**G**-trained: $G_{adj(1)}$ = 0.005; **GR**-trained: $G_{adj(1)}$ = 0.23). Table 6.6 gives the grand totals of **G** and **GG** prey taken from 1:1 populations after training on **G** and after training on **GG**. The data have been pooled because of the relatively low numbers taken from each experiment and because the data from the four experiments appear to be homogeneous. There was a stronger response after training on the **GG** prey type than after training on the **G** prey type, and the two distributions differed significantly ($G_{adj(1)}$ = 4.53, $p<0.05$).

Table 6.7 shows some of the observed data from Table 6.5 broken down into predation by species. The birds did not show very strong responses to training, but in five out of the six sets of data more of the familiar prey type were taken. Where the data could be broken down still further, consistent preferences for the familiar prey type could be demonstrated. Table 6.8 shows the numbers of the two prey types eaten by a blackbird and by a robin in individual bouts of feeding at Site 1 experiment 5a. In the **GG**-trained experiment, the blackbird took more of the **GG** prey type in seven out of eight bouts of feeding ($p = 0.07$, 2-tailed sign test); and in the **G**-trained experiment it took more **G** in four out of six (data insufficient for statistical analysis). This means

TABLE 6.8: Experiment 5b - numbers of **G** and **GG** prey eaten during individual bouts of feeding at Site 1a by a blackbird and by a robin.

	TRAINED ON G Numbers taken		TRAINED ON GG Numbers taken	
	G	**GG**	**G**	**GG**
BLACKBIRD				
1	5	4	7	9
2	6	3	1	5
3	4	1	1	2
4	5	3	5	7
5	1	4	1	3
6	5	5	1	3
7			9	5
8			4	5
TOTAL	26	20	29	39
ROBIN				
1	1	3	1	1
2	1	0	1	0
3	2	1	0	1
4	1	2	1	2
5	1	0	0	2
6			0	1
7			1	0
8			1	4
TOTAL	6	6	5	11

that in eleven out of fourteen bouts the familiar prey type was taken more often (p = 0.058). Similar data for the robin did not show this same consistency (**G**-trained: 3 out of 5 bouts, p = 1.00; **GG**-trained: 5 out of 8 bouts, p = 0.454; in total 11 out of 13 bouts, p = 0.774).

6.3.3 Experiment 5c

Table 6.9 gives the numbers of **G** and **GG** prey eaten during the presentations of the four 1:1 populations, and Table 6.10 gives the numbers of each prey type eaten by sparrows at Site 1 (other predation was either impossible to attribute to individual species or the numbers for each species were too small for statistical analysis). There was no significant heterogeneity between the days of each experiment. At Site 1 there were statistically significant deviations from an expected 1:1 ratio in the **G**-trained experiment, with the familiar prey type being overpredated. In all four experiments more of the familiar prey type was taken. At Site 1 the proportion of the two prey types taken differed significantly between the **G**-trained and **GG**-trained experiments (2 x 2 G tests).

There was no statistically significant heterogeneity between sites when the birds were **G**-trained ($G_{adj(1)}$ = 0.12) or when they were **GG**-trained ($G_{adj(1)}$ = 0.08). Pooling the data again showed that significantly more of the familiar prey type were eaten after training on **G** ($G_{adj(1)}$ = 6.57, $p<0.02$), but, although more of the familiar prey type was eaten after training on **GG**, this difference was not statistically significant ($G_{adj(1)}$ = 2.66). Overall, the proportions of the two prey types taken in the two sorts of experiments differed significantly from one another ($G_{adj(1)}$ = 8.58, $p<0.01$).

The sparrows showed a clear response to training on **G** but not such a clear response to training on **GG**, although in both cases more of the familiar prey types were taken. Significantly different proportions of the two prey types were taken in the two experiments.

TABLE 6.9: Experiment 5c - numbers of G and GG prey eaten from 1:1 populations after training,with values of G_{adj} for a departure from a 1:1 expectation and for independence of the two experiments.

	TRAINED ON G Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON GG Numbers taken		$G_{adj(1)}$ (deviation from 1;1)	$G_{adj(1)}$ (2 x 2, heterogeneity)
SITE	G	GG			G	GG		
1	154	113	6,31*	←	87	109	2,47	7,99**
2	23	19	0,38	→	27	31	0,27	0,65

Arrows indicate order of experiment, Asterisks indicate level of statistical significance; *p<0,02, **p<0,01,

TABLE 6.10: Experiment 5c - numbers of G and GG prey eaten by individual species of birds with values of G_{adj} for a departure from a 1:1 expectation and for independence of the two experiments.

	SPECIES (estimated numbers of birds in parenthesis)	TRAINED ON G Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON GG Numbers taken		$G_{adj(1)}$ (deviation from 1;1)	$G_{adj(1)}$ (2 x 2)
SITE		G	GG			G	GG		
1	Sparrow (15+)	114	76	7,63**	←	61	81	2,82	9,46**

Arrow indicates order of experiment, Astrerisks indicate level of statistical significance; **p<0,01, Unlike the results in Experiments 5a and 5b, which showed a stronger response after training on the striped prey type, there was a higher proportion of **G** prey taken in the **G**-trained experiments than **GG** in the **GG**-trained experiments, but this difference was not statistically significant (Site 1: $G_{adj(1)} = 0.2$; Site 2: $G_{adj(1)} = 0.02$)

6.4 DISCUSSION

The results from these experiments clearly demonstrate that wild birds can acquire preferences for familiar prey that differ only in the presence or absence of a coloured stripe. Past experiments of this type have concentrated on unpatterned prey that differed in colour alone (green and brown pastry prey: Allen and Clarke, 1968; Allen, 1974; red and yellow pastry prey: Oates, quoted by Cook, 1971: 87-88; brown and yellow bread-stuffed *Cepaea* shells, Harvey *et al.*, 1975). As discussed in Chapter 1, the morphs of prey species do not necessarily differ in colour alone: many polymorphic species have morphs differing in their colour patterns. These patterns are very often based on coloured stripes, and in many species there are striped and unstriped morphs (examples are given in Chapter 1).

The effects of training in my experiments were not as strong as they were in earlier experiments by Allen (Allen and Clarke, 1968; Allen, 1974, 1984). For example, Allen (1974), using green and brown pastry baits, observed many trials in which only the familiar prey were eaten. A crucial difference between the design of my experiments and those of Allen was in the degree of similarity between the prey: to humans Allen's brown and green prey types were more distinct in appearance from each other. The prey types used in my experiments had the same ground colour and differed only in the presence or absence of a single coloured stripe. The prey used in Experiments 5b and 5c (plain green, **G** and green-striped green, **GG**) appeared to be more similar to each other than the prey used in Experiment 5a (**G** and red-striped green, **GR**), and the effect of training was apparently decreased in these two experiments. Further experiments by Allen (1984), using a range of plain-coloured prey, confirm that the effect of training is decreased when the prey are more similar in colour.

In my experiments the observed predation was compared to an expected 1:1 ratio. However, in Experiments 2 and 3 (Chapter 4), at densities of 30 prey/m^2 and 4 prey/m^2, the untrained wild birds had a preference for red-striped green (**GR**) over plain green (**G**) and a preference for plain green over green-striped green (**GG**). This preference was probably due to relative conspicuousness, which would go some way to account for the differences in the strengths of the responses after training on **G** and **GR** in Experiment 5a. It is possible that a striped pattern *per se* produces a stronger training response, and this hypothesis appears to be borne out by Experiment 5b where there was also a stronger response after training on the striped prey type than after training on the plain prey type. However, in Experiment 5c, there was a higher proportion of plain prey taken in the plain-trained experiments than striped in the striped-trained experiments, although this difference was slight and not statistically significant.

It is not clear whether the training bias (*cf.* Curio, 1976) arose because the birds acquired a preference for the familiar prey type simply because it was familiar or because they had learned to discriminate it from the background; that is, they had formed a 'search image' (Dawkins, 1971a; Lawrence and Allen, 1983; Bond, 1983). To the human eye, the prey matched their background closely and it would seem that this second explanation is a possible one.

If predators form preferences for familiar (common) forms, rare forms would be at an advantage and selection could be frequency-dependent (Clarke, 1962). The data described in this chapter are further evidence for this type of behaviour, one result of which could be the maintenance of colour-pattern polymorphisms in prey species, even if the morphs are very similar. Chapter 10 further investigates frequency-dependent selection on pattern polymorphisms using a range of prey frequencies and densities. The next chapter reports a series of training experiments that used a range of prey that were even more similar to the human eye than those used in the experiments reported in this chapter: they differed only slightly in the design of their striped colour patterns.

6.5 SUMMARY

1. Previous work has shown that wild birds can become trained to search for a prey type on the basis of its colour. The experiments presented in this chapter extended this work to two types of green artificial prey that were identical except for the presence or absence of a coloured stripe.
2. Wild birds at widely separated sites were trained on populations of one prey type and then were offered a choice between equal numbers of the familiar type and a second type. All the populations were presented on lawn backgrounds. The experiments were then repeated at each site with the birds being trained on the second prey type.
3. There were three experimental series: Experiment 5a used prey types that differed in the presence or absence of a red stripe; Experiments 5b and 5c used prey types that were more similar and differed in the presence or absence of a green stripe.
4. Experiments 5a and 5c used the same time periods for training and for the experimental populations; Experiment 5b used shorter time periods.
5. The results showed that there was a consistent tendency for the familiar prey types to be overpredated and this was statistically significant.
6. The effect of training was decreased when the prey types became more similar (Experiments 5b and 5c) and when the training period was shorter (Experiment 5b); but the effects of training were still of sufficient strength to be statistically significant.
7. The behaviour described in this chapter, if it occurs in nature, could lead to frequency-dependent (apostatic) selection and the maintenance of polymorphism in prey species in which the morphs are distinguished by colour patterns.

CHAPTER 7

EXPERIMENT 7: TRAINING EXPERIMENTS USING VERY SIMILAR PREY - Do wild birds prefer the familiar of prey with very similar colour patterns?

7.1 INTRODUCTION

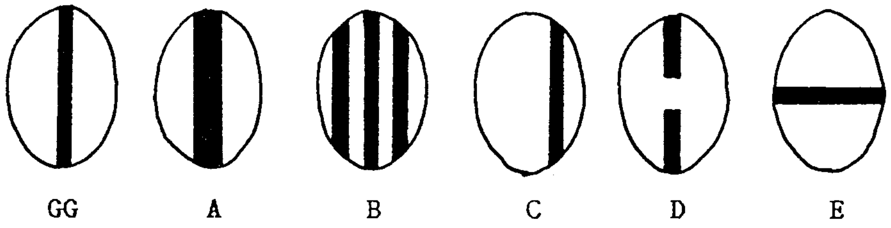
The experiments reported in the preceding chapter clearly showed that wild birds prefer to eat the familiar of striped and unstriped artificial prey. They also showed that this training effect decreases as the prey types become more similar and Allen (1984) has also shown a similar decrease using a range of plain-coloured prey. Experiment 7 was designed to further examine the effects of training by using prey types that were even more similar than those used in Experiments 5a, 5b and 5c (Chapter 6).

It is important to know how specific the birds' responses are to the colour patterns of their prey: many fine details of prey colour patterns have been assumed to be the result of selective pressure by predators (Cott, 1940; Edmunds, 1974; Endler, 1978), also the morphs of many polymorphic prey species are sometimes quite similar (for example, the polymorphic snails, *Cepaea nemoralis* and *C. hortensis*). A range of six prey types was used in Experiment 7 with each prey type differing only slightly in the design of their striped colour patterns and all variations of the green-striped green prey type (**GG**) used in previous experiments (Chapters 4 and 6). Each prey type had the same ground colour and a striped pattern that was also of the same colour but which varied from that of the **GG** prey in a different way (such as a change in direction of stripe, in the number of stripes or in the thickness of stripe). These prey types were designed to test if particular variations in colour patterns could be detected by the birds and whether these different prey patterns affected the outcome of training experiments. Pairs of these prey types, one of which was always **GG**, were used in a series of training experiments with one group of birds from one site. The birds at this site were also given choice tests of equal numbers of all the prey types to see if the birds had any prey preferences. These choice tests were used as controls for the training experiments.

7.2 MATERIALS AND METHODS

7.2.1 Prey

All the prey types had the same green ground colour and the same green stripe colour, which were those of the green-striped green prey type used in previous training experiments (GG: Experiments 5b and 5c, Chapter 6; see Plate 4.1, Chapter 4). GG was one of the prey types used in this series of training experiments and the other five prey type had colour patterns that were all variations on the basic colour pattern of GG: a single longitudinal green stripe, centrally placed, 2mm wide. Prey type **A** had a stripe that was twice as wide as that of GG; prey type **B** had three stripes instead of one; prey type **C** had a single stripe that was off-centre; prey type **D** had a 4mm gap in the centre of the stripe; and prey type **E** had a transverse stripe instead of a longitudinal one.



GG: Prey with central longitudinal stripe. Stripe 2mm width.

A: Variation in the width of the stripe. Stripe 4mm width.

B: Variation in the number of stripes. 3 stripes. Stripes 2mm width. 2mm gap beween stripes.

C: Variation in the position of the stripe. Stripe off-centre.

D: Variation in the stripe. 4mm gap in the centre of the stripe.

E: Variation in the direction of the stripe. Transverse stripe.

7.2.2 Background and Site

The prey populations were presented on grass lawn at the Medical and Biological Sciences Building (Boldrewood), Southampton University (Site 1 in Experiment 5b, Chapter 6).

TABLE 7.1: Experiment 7 - species of birds observed feeding in each set of experiments. For scientific names see Table 2.1.

	EXPERIMENT			
	CONTROLS		SERIES	
SPECIES	1	2	1	2
Blackbird	+	+	+	+
Robin	+	+	+	+
Woodpigeon	+	+	+	+
Magpie	+	+	+	+
Collared dove	-	+	+	+
Chaffinch	-	+	-	+

7.2.3 Predators

Table 7.1 gives a list of the species of birds observed feeding during each experiment.

7.2.4 Procedure

There were two sets of training experiments. In the first set (Series 1), the birds were always trained on the green-striped prey type (**GG**), and then were given a choice between this and one of the other prey types. In the second set (Series 2), the birds were trained on one of the other five prey types (**A** - **E**), and then were given a choice between that particular prey type and the **GG** prey type. So that there could be direct comparison between the two sets, the order in which the prey types **A** - **E** 'partnered' the **GG** prey type was chosen at random and was the same in the two sets of training experiments. The order was: **A, D, C, E, B.**

The method used in these experiments was the same as that used in the previous training experiments, and is described in Chapter 6. The training period was two days. 500 training prey were eaten in each experiment. The populations containing equal numbers of the two prey types were presented for seven hours in Series 1 and, because of the shorter hours of daylight and weather problems, for a shorter period (between two and four hours) in Series 2. Series 1 ran from 15th August - 22nd September 1983, and Series 2 ran from 8th November - 15th December 1983.

The method used for obtaining the prey distributions is described in Chapter 6. The prey were placed in their allocated positions by the method used in other experiments: they were dropped from waist height and then adjusted where necessary so that they were level and their colour patterns uppermost.

To control for any preferences that the birds might have had for the prey, two sets of choice tests were done. All six prey types were presented simultaneously to the birds on a grid marked out on the lawn. The grid was 5m x 6m and the prey were presented at a density of 2 prey/m^2, thus making a population size of 60 prey. The prey distributions were determined using playing cards for the first control

TABLE 7.2: Totals of each prey type taken in the two control experiments in Experiment 7 with values of G_{adj} for a departure from a 1:1:1:1:1:1 expectation. None of the values of G_{adj} were statistically significant.

	Numbers taken						
	GG	A	B	C	D	E	
CONTROL							$G_{adj(5)}$ (deviation from 1:1 etc)
1	10	13	13	10	14	17	2.65
2	91	102	88	98	93	108	2.86
Total	101	115	101	108	107	125	3.80

TABLE 7.3: Totals of each prey type taken from 1:1 populations after training and the percentages of the training prey eaten in Experiment 7, with values of G_{adj} for a departure from a 1:1 expectation, for heterogeneity within each set of experiments and for independence of the experiments using the same pair of prey types. None of the values of G_{adj} were statistically significant.

SERIES 1				SERIES 2				
Numbers taken TRAINED ON ↓		Percentage training prey taken	$G_{adj(1)}$ (deviation from 1:1)	Numbers taken TRAINED ON	↓	Percentage training prey taken	$G_{adj(1)}$ (deviation from 1:1)	$G_{adj(1)}$ (2 x 2)
								
31	27	53,45%	0,27	55	64	53,78%	1,14	0,81
								
16	15	51,61%	0,003	70	53	43,09%	2,35	0,28
								
55	50	52,34%	0,24	52	65	55,56%	1,44	1,39
								
55	62	47,01%	0,42	52	56	51,85%	0,15	0,03
								
18	22	45,00%	0,40	87	100	53,48%	0,90	0,03

G tests for heterogeneity within the two sets of experiments:

SERIES 1: $G_{adj(4)} = 1,35$ N.S.
SERIES 2: $G_{adj(4)} = 4,78$ N.S.

experiment (Control 1), and then by using a BASIC computer program, similar to that used in Experiment 5c (General Appendix A), for the second control experiment (Control 2). The prey were placed in their allocated positions on the lawn using the method described above for the training experiments. Control 1 was done on the 27th October 1983, one month after the first series of training experiments (Series 1), and the birds were presented with one prey distribution. Control 2 lasted for nearly a month, 2nd February - 1st March 1984, about six weeks after the end of the second series of training experiments (Series 2), and twelve different prey distributions were used.

As in the training experiments, the prey populations were watched and the species of birds observed feeding were recorded. Whenever possible, the movements of the birds across the grid were recorded by sketching them onto copies of the grid. Eaten prey were recorded and replaced after a bout of feeding; if more than 35 prey had been eaten, such trials were disregarded from later analysis.

7.3 RESULTS

Table 7.2 gives the numbers of the six prey types eaten during the two control experiments. There were no statistically significant preferences for any of the prey types and there was no significant heterogeneity between the two control experiments ($G_{adj(5)} = 1.73$).

Table 7.3 gives the totals of each prey type taken in the ten training experiments. There were no statistically significant deviations from an expected 1:1 ratio. Furthermore, the familiar form was not consistently overpredated: although more training prey type were taken in 7 out of 10 experiments this was not statistically significant ($p = 0.344$, sign test).

In Series 1, where the birds were trained on the same prey type (**GG**) for the five experiments, there was a decrease in the proportion of the familiar prey type (**GG**) eaten from the 1:1 populations as the Series progressed. Regression analysis (on normalised data - arc-sin transformed proportions) showed a significant linear regression of the proportion of GG prey eaten against time ($b_{x.y} = -1.24$, $S_b = 0.29$, $t_s = 4.27$ $p<0.05$, Sokal and Rohlf, 1981). The totals of each prey type taken in the experiments were made up of numbers of each prey type taken in bouts of feeding before replacement. The proportion of bouts in each experiment in which the training prey were taken the most can be analysed using Spearman's Rank Correlation (Siegel, 1956) and the results confirmed those obtained from the regression analysis above ($r_s = 1$, $N = 5$, $p = 0.02$).

Similar analysis was performed on the results from Series 2. No trend with time was detected ($b_{x.y} = 0.47$, $S_b = 0.99$, $t_s = 0.47$ N.S. and $r_s = 0.225$, $N = 5$, N.S.).

7.4 DISCUSSION

The control experiments showed that the birds had no significant preferences for any of the prey types. This lack of preferences could have been because the birds could not distinguish between the very similar prey types, alternatively, that they could but there was no selective feeding because the prey types were all found equally easily, inasmuch that they were all generally equally conspicuous/cryptic. The results from the training experiments seemed to indicate either that the birds could not distinguish between the prey types or that they could, but that the training periods did not affect their subsequent feeding behaviour.

If the birds could not distinguish between the different prey types, then it would be expected that training on one prey type would not influence predation. When the birds were afforded a choice of the very similar prey types, they did not significantly overpredate the original prey type offered in training. The results from the ten training experiments supported this overall impression. However, in Series 1, where the birds were trained in all five experiments on the same prey type, there was a decrease in the proportion of the training prey eaten as the series progressed. This was confirmed by regression analysis on both the total numbers of the prey types eaten in each experiment and on the individual bouts of feeding that made up these totals. This result suggests that the birds **could** distinguish between the prey types. The direction of the regression (negative) was the opposite to what might have been predicted by the hypothesis of 'training bias': as the birds grew more and more familiar with the **GG** prey type (they ate over 2500 **GG** prey in total in the few days before the last experiment in this Series) they should have eaten a greater proportion of **GG** in each trial. This prediction is based on the results from other training experiments (see Chapter 6 and the introduction for this chapter). The result could possibly have been caused by the order in which the pairs of prey were presented: if, by chance, they had been presented in the order of increasing conspicuousness of the non-training prey types, then a decrease in the proportion of the **GG** prey type taken as the series progressed would have been expected.

Series 2 did not show consistent changes with time. However, the training prey type varied throughout the series; therefore this series was not an 'opposite' to Series 1 and could not be compared directly to it. However, if the regression in Series 1 was the result of the order of the experiments then a similar decrease in the proportion of **GG** prey eaten across the experiments would be expected in Series 2. This was not the case and therefore it seems more likely that the regression observed in Series 1 was due to a response to familiarity with **GG**. The differences between the numbers of the two prey types taken in each experiment were small and therefore the regression should not be over emphasised. Nevertheless, it indicated an opposite response to those observed in most past training experiments where the familiar prey type has been overpredated (Allen and Clarke, 1968; Allen, 1974, 1984; Croze, 1970; Harvey, Birley and Blackstock, 1975; Raymond, 1984).

However, Bryan (1973), in his training experiments using trout (*Salmo gairdneri* Richardson) as predators, tubifex (*Tubifex* sp.) and brine shrimp (*Artemia salina* (L.)) as prey, found that the trout ate a greater proportion of the training food type in most experiments but, in some instances, found that highly significantly fewer of the training prey type were eaten. For example, in Experiment 3, the total numbers of each prey type taken by all trout in their first test meal were 21 shrimp and 7 tubifex for trout trained on dead tubifex and 24 shrimp and 57 tubifex for trout trained on dead shrimp, resulting in a highly significant difference between the two results ($p<0.001$, χ^2 (2x2)). Bryan suggests that this result was due to the particular experimental design: "Training biases were not evident, however, when trout were trained in groups of three within plastic containers. Some effect of group size, container size, or both, presumably prevented either development or expression of training biases in this situation".

One possible explanation for the results obtained in the series of experiments reported in this chapter (and also possibly those of Bryan, 1973), is that the birds were choosing a mixed diet. Tinbergen (1960) observed that great tits did not have a monotonous diet even when one prey species was very abundant. There were no apparent differences between the prey types in Experiment 7 in terms of profitability and handling times, and the differences in conspicuousness might have been insignificant to the birds; the birds might then have been optimising their diets (theoretically although not actually) by choosing increasingly fewer of the **GG** prey. Since the prey types were so similar to each other, novelty of the non-training prey types might not have influenced the birds' feeding behaviour. Clearly, further work is needed to determine whether, after repeated training on the same prey colour pattern, avoidance of a familiar prey type occurs consistently increasingly with time.

7.5 SUMMARY

1. Chapter 6 showed that wild birds prefer to eat the familiar of striped and unstriped artificial prey but that this effect decreases as the prey types become more similar. The experiments presented in this chapter extended this work further by using prey types that were even more similar to each other.
2. Six prey types were used, one of which was the green-striped prey type (**GG**) used in Experiments 6b and 6c. All the prey types had various green-striped patterns.

3. Wild birds at one site were trained on populations of one prey type and then were offered a choice between equal numbers of the familiar type and a second type.

4. In all the experiments one of the prey types was **GG**. There were two series of experiments: Series 1 where the training prey type was **GG** in all five experiments; Series 2 where the training prey was different in the five experiments.

5. Choice tests to control for preferences for any of the prey types were done. No preferences were found.

6. In Series 1 there appeared to be no response to training: there was no overpredation of the familiar prey type (**GG**). There was a decrease in the proportion of **GG** prey taken across the Series and this regression was statistically significant. The direction of this regression is the opposite to that which would be predicted: it appeared that as the birds became more and more familiar with the **GG** prey type they took proportionally more of the unfamiliar prey types when given a choice.

7. The results from Series 2 showed no overpredation of the familiar prey types and no trend with time.

CHAPTER 8

EXPERIMENT 4: CHICK TRAINING EXPERIMENTS USING SIMILAR PREY - Do individual chicks prefer the prey type that is most similar to a familiar prey type?

8.1 INTRODUCTION

Past training experiments have showed that, when given a choice between prey types, birds usually prefer to eat the familiar type (Allen and Clarke, 1968; Allen, 1974, 1984; Croze, 1970; Harvey, Birley and Blackstock, 1975; Raymond, 1984). In all these experiments, the birds were given a choice that included a prey type which they had experienced previously.

Croze (1970) found that the previous feeding experience of crows affected the specificity of their choice of prey. The crows were offered a choice between prey (mussel shells painted red and filled with meat) that were familiar to them and prey that were similar but differed in terms of colour, shape or structure. The crows were specific in their preferences and chose the shells that were familiar. Other training experiments have used prey type that differed in respect to colour (Allen and Clarke, 1968; Allen, 1974, 1984; Harvey *et al.*, 1975) or size (Harvey *et al.*, 1975). All found that the most familiar prey type was preferred by bird predators. Such behaviour by visually hunting predators might result in overpredation of common prey types and result thus in the maintenance of colour polymorphisms.

If, after feeding from one prey population, a predator acquired a preference for a particular prey type (perhaps because it was common) and then moved to feed on another, perhaps adjacent, prey population comprising different prey types, it might generalise that preference and then proceed to feed predominantly on the prey type that most closely resembled the prey type preferred originally. The result of this might be that the frequencies of prey types with similar colour patterns in adjacent prey populations would be negatively-correlated.

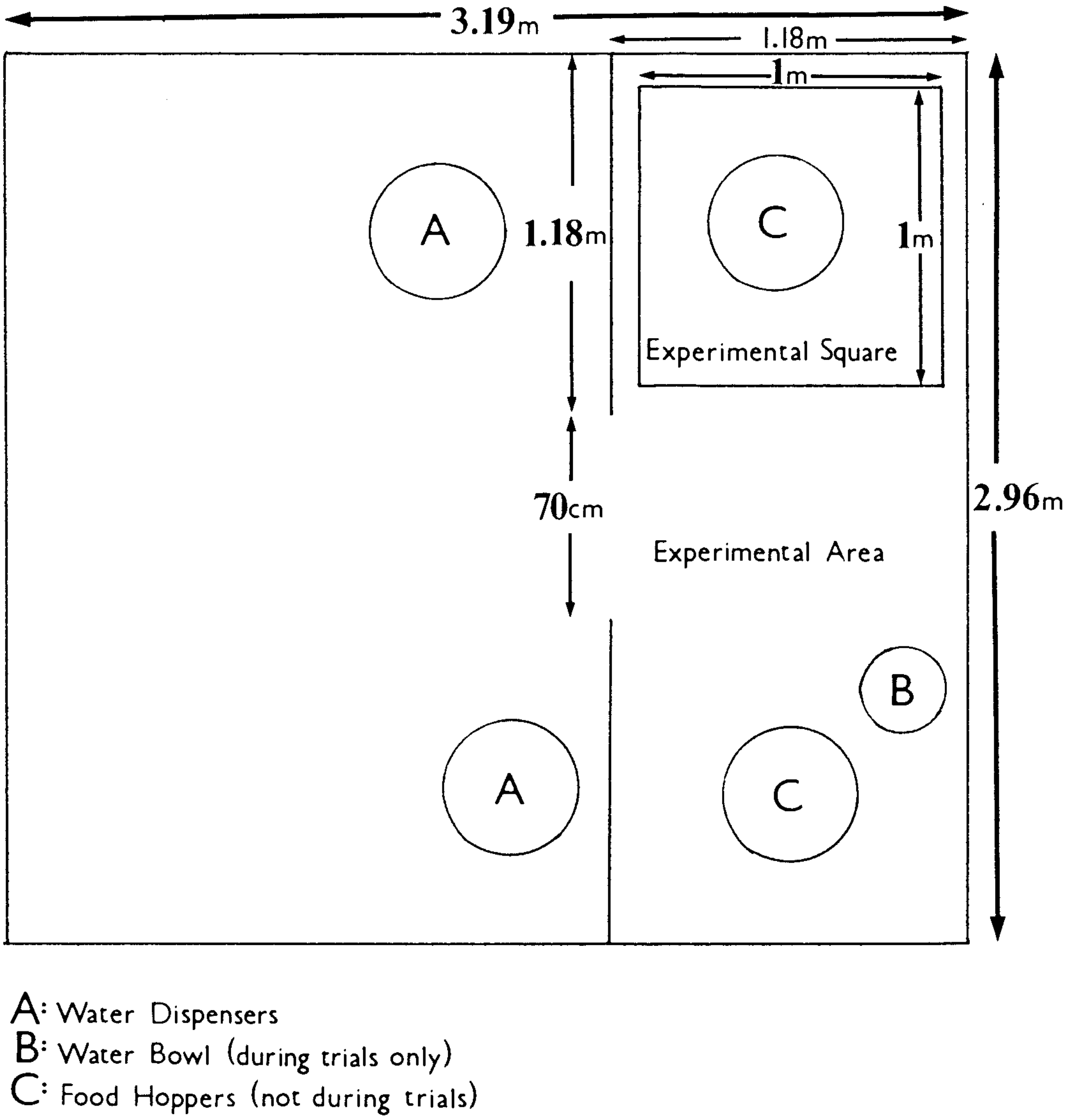
The experiment reported in this chapter was designed to see if predators would select the prey type that was the most similar to a prey type that they were familiar with through training, from a choice of three prey types that did not include the 'training' prey type. All 'experimental' prey differed from the training prey type in respect to ground colour; one also differed in respect to colour pattern and one in respect to shape. The birds were given a pre-training choice test of the experimental prey types to control for any preferences. The birds were then given a period of feeding on the training prey type and then again given a choice between the experimental prey types. In order to monitor prey selection by individual predators, chicks under controlled conditions were used rather than wild garden birds. The use of known individuals meant that information such as the first prey type eaten by each chick could be recorded and comparisons made between pre-training and post-training trials. Their past experience of food types could be controlled and large numbers of chicks were available for experimentation. Chicks have been used successfully in past predation experiments (eg., Capretta, 1969; Dawkins, 1971a,b).

8.2 MATERIALS AND METHODS

8.2.1 Prey

The prey types were four of the prey types described in Chapter 2, Table 2.2. One 'training' prey type and three 'experimental' prey types were used. The training prey type was a white pastry oval. The experimental prey were all coloured yellow. Two were oval, one plain (**YO**) and one with a single longitudinal dark yellow stripe (**YY**), and the third was plain and star-shaped (**YS**). Thus, the three experimental prey types differed from the training prey type: they all had a different ground colour from the training prey; one was also a different shape and one had a different colour pattern. The experimental prey type that was the most similar to the training prey therefore appeared to be the **YO** prey type because it only differed in respect to ground colour.

FIGURE 8.1: **Experiment 4** - Plan of experimental area.



8.2.2. Predators

Twenty nine one-month-old male domestic chicks (strain: "Ross Brown") were used. Four of these were used as 'companion chicks' during experimental trials since single chicks would not feed and became distressed (Dawkins, 1971a)

8.2.3 Background and Site

The chicks were kept in an outhouse at Chilworth Manor, Southampton (O.S. reference: SU 405185), in an area 3.19m x 2.96m. The floor was flagstones covered in straw. An area 1.18m from one wall was divided off, using hardboard, with a gap 0.70m wide, 1.18m from one end. A square area 1m x 1m was marked out with permanent felt pen on the floor at one end. (Fig. 8.1).

The gap was left open except during experimental trials, allowing the chickens a free run of the whole area outside experimental hours. During this time, the hoppers of chick crumbs (the staple food of the chicks) were kept in the experimental part of the enclosure, which meant that the chicks associated this area with food. The food hoppers were removed about one hour before the start of the first experimental trial in order to increase the chances of the chicks feeding and also to ensure that they only fed on the experimental prey. The gap was blocked with a piece of hardboard during experimental hours and the chicks prevented from entering the experimental area.

During the experiments the floor of the experimental square was swept clear of straw, leaving the flagstones to act as a background for the prey.

The experimental square could be blocked off with hardboard from the rest of the experimental area so as to control the chicks' access to the prey during experimental trials.

A bowl of water was placed in the experimental area during trials to ensure that the chicks always had access to water.

8.2.4 Procedure

The experiment ran over eleven days from the 8th to 18th November 1982. Each experimental chick experienced a pre-training choice trial in which equal numbers of the three yellow prey types were presented to control for any preferences, a period of training on the white prey type alone and then a post-training choice trial to test for any changes in preferences as a result of the period of training.

The gap between areas was blocked with all the chickens outside the experimental area. Four chicks were caught and marked (by colour-ringing) for use as companion chicks.

Ten of each of the three yellow prey types were placed at random on the experimental square: a density of 30 prey/m^2. The experimental square was then shut off. A chick from the experimental group was caught, colour-ringed, and introduced with one of the companion chicks into the experimental area. The barrier to the experimental square was removed and the chicks allowed to feed. The prey eaten by the experimental chick were recorded in the order in which they were taken and the trial was stopped when it had eaten about ten prey. Some chicks ate less than ten prey and then became disinterested in the food; if this happened, the trial was concluded. Unfortunately, it was impossible to record what prey the companion chick ate because feeding usually continued while the chicks were being recaptured, and missing prey (but not recorded as having been eaten by the experimental chick) could not necessarily be attributed to the companion chick.

This procedure was repeated until all the experimental chicks had been used (in a random order). The companion chick was changed after two or three trials so that each had approximately the same number of trials per day. The pre-training trials were carried out over a period of three and a half days.

The training period started immediately all the pre-training trials had finished. 160 prey were fed to the chicks each day for six days. The prey were scattered on the floor of the experimental area once each day and the chicks were allowed to feed freely. During this training period the chicks had continuous access to chick crumbs because the

TABLE 8.1: Raw data for Experiment 4. Pre-training trials (8th - 10th November 1982).

CHICK (Companion Chick)	PREY EATEN
1(A)	YY, YY, YY, YS, YO, YS
2(A)	YY, YO, YO, YY, YS, YS
3(C)	YS, YY, YS, YS, YS, YS, YS, YO, YO, YO
4(B)	YY, YO, YY
5(D)	YY, YO, YO, YO
6(D)	YO, YY, YS, YO, YO, YS, YO, YY, YS, YO
7(D)	YO, YY
8(C)	YY, YS, YO, YO, YS
9(B)	YY, YY, YS, YS, YY, YY, YS, YS, YS, YO, YO, YO, YS
10(B)	YY, YO, YO, YO, YS, YS, YS, YS, YS, YS, YS
11(B)	YS, YY, YY, YY, YS, YY, YS, YY, YO, YS
12(A)	YS, YY, YS, YO, YO, YS, YS, YY
13(A)	YY, YS, YY, YO, YO, YS, YO, YS, YY, YY, YO
14(A)	YO, YY, YS, YO, YS, YY, YS, YS, YO, YS, YY, YY
15(A)	YY, YO, YO, YS, YY, YY, YS, YY, YO, YY
16(D)	YS, YY, YY, YY, YO, YY, YY
17(D)	YY, YY
18(C)	YY, YS, YO, YS, YY, YO, YS, YY, YY, YY, YO, YS
19(C)	YO, YO, YS, YS, YY, YS, YO, YY, YO, YS, YY, YO
20(B)	YY, YY, YO, YY, YS, YO, YY, YO, YS
21(B)	YS, YS, YO, YO, YY, YY, YS, YY, YS, YY
22(C)	YO, YS, YY, YS, YO, YS, YY, YS, YS, YO, YS
23(C)	YO, YS, YY, YS, YS, YS, YS
24(D)	YS, YO, YY, YO, YY, YY, YS, YO, YY, YO
25(D)	YS, YY, YY, YY, YS, YY, YY, YO, YS, YS

TABLE 8.2: Raw data for Experiment 4. Post-training trials (17th - 18th November 1982)

CHICK (Companion Chick)	PREY EATEN
1(A)	YO, YY, YO, YO, YO, YS, YS, YY, YO, YO, YO, YS
2(A)	YY, YO, YS, YY, YO, YO, YO, YS, YY, YY, YO
3(C)	YO, YY, YS, YO, YY, YY, YY, YS, YS, YO, YS
4(B)	YO, YO, YS, YY, YO, YY, YY
5(D)	YY, YO, YY, YS, YO, YO, YO, YY, YO, YY, YO, YO, YO
6(D)	YO, YO, YS, YY, YY, YY, YO, YY, YY, YY, YS
7(D)	YY, YO, YS, YY, YS, YS, YS, YY, YY, YO
8(C)	YO, YO, YY, YS, YO, YS, YY, YY, YS
9(B)	YO, YY, YO, YO, YS, YO, YO, YO, YS, YO, YY, YS
10(B)	YS, YS, YO, YY, YS, YY, YS, YY, YY, YO, YO, YS
11(B)	YO, YO, YS, YS, YO, YY, YO, YO, YY, YO, YS
12(A)	YO, YO, YY, YS, YO, YS, YS, YY, YY, YS, YO
13(A)	YO, YS, YO, YS, YS, YS, YO, YY, YY, YS YS
14(A)	YY, YY, YS, YO, YY, YS, YO, YS, YO, YS
15(A)	YY, YS, YO, YO, YY, YS, YS, YO, YY, YS, YS
16(D)	YO, YY, YY, YO, YY, YY, YO, YS, YO, YY
17(D)	YY, YS, YY, YY, YY, YO, YO, YY, YY, YY, YO
18(C)	YS, YY, YY, YO, YS, YS, YY, YS, YO, YO
19(C)	YY, YO, YS, YY, YO, YY, YS, YO, YY, YS, YO
20(B)	YS, YY, YO, YY, YS, YY, YO, YS, YY, YO, YS
21(B)	YO, YS, YY, YY, YS, YS, YO, YY, YS, YO, YS, YO, YS, YO, YO
22(C)	YY, YO, YS, YO, YY, YS, YO, YY, YY, YY, YO, YS, YO, YO
23(C)	YO, YS, YY, YY, YS
24(D)	YY, YS, YY, YY, YY, YS, YY, YO, YO, YO, YS
25(D)	YS, YO, YS, YO, YS, YY, YY, YO, YY, YS, YY

pastry prey could not be made in sufficient quantity to be the only source of food. It was also questionable whether pastry alone would have been nutritionally sufficient for the chicks. The chicks ate the training prey fairly quickly and therefore this food was not available to them throughout the training period.

At the end of the six day training period the chicks were given the post-training choice trials. The same procedure was used as for the pre-training trials with the addition that, immediately prior to the trial, each experimental chick was given ten white oval prey to ensure similar immediate pre-trial experience for all the chicks. The chicks were tested in the order in which they were caught, which differed from the order of the pre-training trials. They were tested with the same companion chick that they had had in the pre-training trials. The post-training trials were carried out over a period of two days.

8.3 RESULTS

Tables 8.1 and 8.2 give the order in which the prey types were eaten in the pre-training and post-training trials. So that direct comparison could be made between pre- and post-training trials for each chick, prey eaten in the post-training trials that were recorded but which resulted in a different total number of prey eaten from that in the pre-experimental trials, were excluded from further analysis. Table 8.3 gives the resulting total numbers of each prey type taken and which prey type was the first taken, for each chick.

Analysis for heterogeneity by G test was not legitimate because of the low numbers, but inspection of the data suggested that they were not particulary heterogeneous. Using the grand totals of each prey type eaten, there was no statistically significant deviation from a 1:1:1 ratio either before or after the training period (pre-training: $G_{adj(2)}$ = 2.126; post-training: $G_{adj(2)}$ = 1.948). There was an increase in the number of plain ovals (**YO**) eaten in the post-training trials but this was not statistically significant: the proportions eaten for the two sets of trials were not significantly different from each other ($G_{adj(2)}$ = 3.570).

TABLE 8.3: Total numbers of each prey type eaten by each chick (matched to give the same total number of prey eaten for each chick) in the pre-training and post-training choice trials in Experiment 4, together with the prey type eaten first by each chick in the two sets of trials.

	PRE-TRAINING					POST-TRAINING				
	PREY TYPE				1ST	PREY TYPE				1ST
CHICK	**YO**	**YY**	**YS**	TOTAL	EATEN	**YO**	**YY**	**YS**	TOTAL	EATEN
1	1	3	2	6	YY	4	1	1	6	YO
2	2	2	2	6	YY	3	2	1	6	YY
3	3	1	6	10	YS	3	4	3	10	YO
4	1	2	0	3	YY	2	0	1	3	YO
5	3	1	0	4	YY	1	2	1	4	YY
6	5	2	3	10	YO	3	6	1	10	YO
7	1	1	0	2	YO	1	1	0	2	YY
8	2	1	2	5	YY	3	1	1	5	YO
9	3	4	5	12	YY	7	2	3	12	YO
10	3	1	7	11	YS	3	4	4	11	YS
11	1	5	4	10	YS	6	2	2	10	YO
12	2	2	4	8	YS	3	2	3	8	YO
13	4	4	3	11	YY	4	2	5	11	YO
14	3	2	5	10	YO	3	3	4	10	YY
15	3	5	2	10	YY	3	3	4	10	YY
16	1	5	1	7	YS	3	4	0	7	YO
17	0	2	0	2	YY	0	1	1	2	YY
18	2	5	3	10	YY	3	3	4	10	YS
19	4	3	4	11	YO	4	4	3	11	YY
20	3	4	2	9	YY	2	4	3	9	YS
21	2	4	4	10	YS	3	3	4	10	YO
22	3	2	6	11	YO	4	5	2	11	YY
23	1	1	3	5	YO	1	2	2	5	YO
24	4	4	2	10	YS	3	5	2	10	YY
25	1	5	4	10	YS	3	3	4	10	YS
TOTAL	58	73	72	203		75	69	59	203	

TABLE 8.4: Totals of **YO** and **YY + YS** prey types taken in the pre-training and post-training trials.

TRIALS	TOTAL EATEN **YO**	 **YY + YS**	TOTAL
PRE-TRAINING	58	145	203
POST-TRAINING	75	128	203
TOTAL	133	273	406

TABLE 8.5: Number of times each prey type was taken first in the pre-training and post-training trials.

TRIALS	FIRST EATEN **YO**	 **YY**	 **YS**	TOTAL
PRE-TRAINING	6	12	7	25
POST-TRAINING	12	9	4	25
TOTAL	18	21	11	50

TABLE 8.6: Totals of the first prey type taken with **YY** and **YS** totalled together.

TRIALS	FIRST EATEN **YO**	 **YY + YS**	TOTAL
PRE-TRAINING	6	19	25
POST-TRAINING	12	13	25
TOTAL	18	32	50

Since the **YO** prey type appeared to be the most similar to the training prey type (they differed only in respect to ground colour), it was decided to test for a change in the proportion of **YO** eaten against both the other two prey types. The totals for the striped prey type (**YY**) and for the star prey (**YS**) were grouped together for further analysis (Table 8.4). An increased preference for **YO** in the post-training trials when compared with the pre-training trials is suggested ($G_{adj(1)}$ = 3.224, p<0.1).

Table 8.5 shows how often each prey type was taken first in both sets of trials. Although the **YO** prey type was taken first twice as often in the post-training trials than in the pre-training trials, this was not statistically significant ($G_{adj(2)}$ = 3.16). In order to test for change in the numbers of **YO** taken first compared with both the other two prey types, the totals for **YY** and **YS** were again added together (Table 8.6). There was some evidence that there was an increase in the number of **YO** prey taken first in the post-training trials (p = 0.051, Fisher exact test, Siegel, 1956).

8.4 DISCUSSION

The results from this experiment found a small increase in the number of plain oval yellow prey (**YO**) eaten after training on white oval prey, both in the total taken and in the first eaten when compared with the numbers taken in the pre-training trials.

It is possible, in the post-training trials, that the chicks acquired a preference for the prey type that was the most similar to the prey type used in the training period. Out of the three yellow prey types,**YO** fitted this criterion the best. If so, it would seem that the outline of the prey was a factor that affected the feeding behaviour of the chicks: fewer star-shaped prey were taken in the post-training trials than in the pre-training trials. The outline of a prey item is thought to be recognised by predators that hunt by sight, and a characteristic body outline is sometimes broken up by projections which conceal the shape (Edmunds, 1974). Colour patterns may also act to disrupt the outline of a prey item (Cott, 1940; Edmunds, 1974). The fact that fewer striped prey were eaten could indicate that the stripe acted to disrupt the outline of the prey, making it thus unrecognisible as a familiar oval prey type. On the other hand, the striped colour pattern might have just reduced the striped prey type's similarity to the training prey type.

Previous training experiments (including those in Chapters 6, 7 and 9) have always included the training prey type in the post-training choice tests (Allen and Clarke, 1968; Allen, 1974, 1984; Croze, 1970; Bryan, 1973; Harvey, Birley and Blackstock, 1975; Raymond, 1984) and therefore direct comparison between these experiments and the experiment reported in this chapter is not possible. However, the same essential prediction that the birds would prefer to eat the prey type most similar to a prey type that they were familiar with holds for both types of experiment: nothing is more similar than identical prey types.

One of the problems with this experiment was the necessity for there to be a 'companion chick' present with the experimental chick during trials. Because the prey population was small, this meant that any feeding by the companion chick resulted in a depletion of the prey available to the experimental chick. If the companion chick showed a preference for one of the prey types, the result would be that fewer of that particular prey type would be available to the experimental chick, which might result in it being forced to eat more of the other two prey types. Therefore, if both chicks had acquired preferences for the same prey type (for example, **YO**) then there would be competition for this prey type in the trials, and this would result in a less obvious preference by the experimental chick for that prey type and, consequently, a less significant statistical result. But, to ascertain if this was happening, the predation of both chicks in relation to each other needed to be recorded, which would have required more (unavailable) manpower or video recording equipment. The counting of remaining prey was not a practicable alternative since the chicks continued to feed after the trial had been stopped, and in some trials often there were no remaining prey.

8.5 SUMMARY

1. Previous experiments have shown that when given an equal choice birds prefer a familiar prey type. In all these experiments, the birds were given a choice of prey that included a prey type they had experienced before. The experiment reported in this chapter was designed to test whether birds would select, from a choice of equal numbers of different prey types, the prey type that was the most similar to a prey type that they were familiar with through training.
2. Four prey types were used. The 'training prey type' was a plain white oval. The prey used in the choice tests were a plain yellow oval (**YO**), a yellow oval with a yellow stripe (**YY**) and a plain yellow star (**YS**).
3. The birds were twenty nine one month old domestic chicks. Four of these were used as 'companion chicks' during experimental trials.
4. Each chick was given a pre-training choice test on the three yellow prey types to control for any preferences. This was followed by a communal training period of five and a half days on the white oval prey. There was then a post-training choice test for each chick.
5. There were no statistically significant preferences for any of the three yellow prey types either before or after the training period.
6. There was an increase in the total number of plain yellow ovals (**YO**) eaten in the post-training trials but this was not statistically significant. However, a change in the proportion of **YO** eaten against both the other two prey types is indicated.
7. Analysis of which prey type was taken first by each chick in each of their two trials, indicates a trend towards the **YO** prey type being taken first more often in the post-training trials than in the pre-training trials.
8. It is suggested that the chicks acquired a preference for the prey type that was the most similar to that used in the training period, although the possibility that they were searching using the outline (shape) of the prey as a cue and that the stripe on the striped prey served to disrupt this outline are also discussed.
9. The problems encountered with the design of this experiment, especially those resulting from the use of companion chicks, are also discussed.

CHAPTER 9

EXPERIMENT 10: TRAINING EXPERIMENTS USING BANDED AND UNBANDED *CEPAEA HORTENSIS* (Mull) SHELLS - Do garden birds prefer the familiar prey type?

9.1 INTRODUCTION

In Chapter 6, experiments were reported that showed wild birds preferred the familiar of striped or unstriped artificial prey types after training. Inspired by an experiment by Harvey, Birley and Blackstock (1975), in which song thrushes were fed on either yellow or brown unbanded "bread-stuffed" *Cepaea nemoralis* (L.) shells, it was decided to repeat the basic experimental design described in Chapter 6 using pastry-filled Yellow Five-banded and Yellow Unbanded *Cepaea hortensis* (Mull) shells. It was hoped that this would extend the experimental designs used so far to a more 'natural' situation to try to test "whether sight-dependent predators can be trained to search for a particular morph of a natural polymorphic species" (Allen, 1974, 1984). *Cepaea* morphs are real examples of variations in colour patterns and, in general, snails would be familiar, whether or not as potential prey, to most garden birds. There would also be a degree of variation within each colour-pattern group, which would be found in real snail populations, that was not present in the pastry prey experiments.

9.2 MATERIALS AND METHODS

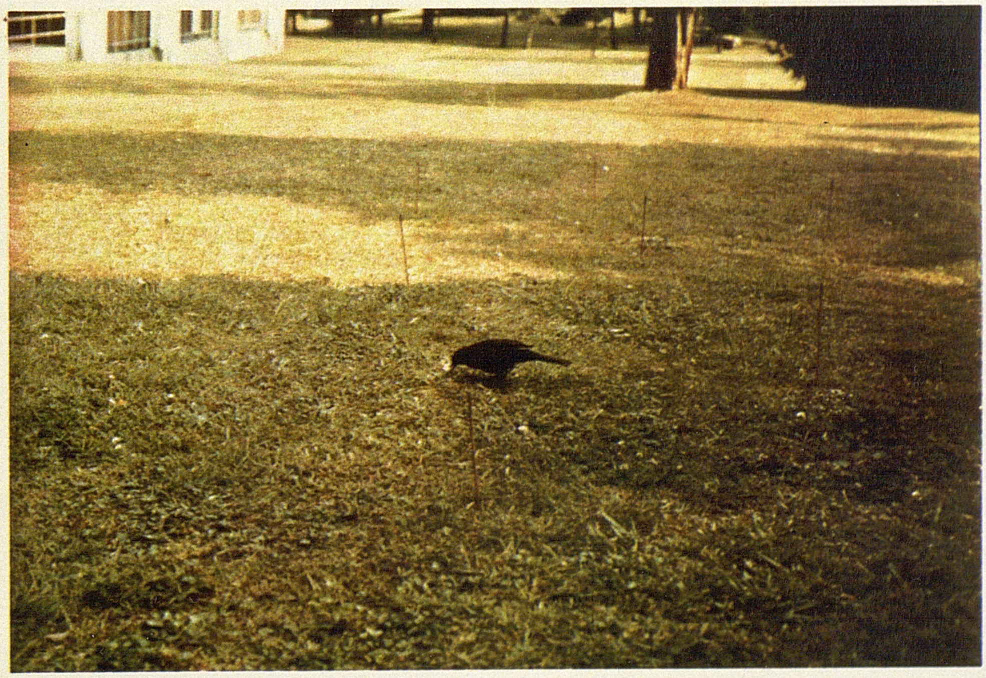
9.2.1 Prey

Cepaea hortensis shells filled with uncoloured (white) pastry were used as the prey in this experiment. The pastry was made using the method described in Chapter 2. There were two shell types: Yellow Unbanded (**YU**) and Yellow Five-banded (**Y5**) (Plates 9.1 and 9.2).

The shells were obtained from a number of different populations. Both groups of morphs were composed of shells from at least five

PLATE 9.1: Experiment 10. Example of two *Cepaea hortensis* shells on the grass background at Site 1: **YU** (left) and **Y5** (right).

PLATE 9.2: Experiment 10, Site 1. Female blackbird attacking a snail shell.



populations. The shells were mixed together and used at random. Two different groups of shells were used for the experiments at the two sites (see Section 9.2.2 below). Since no living snails were used in these experiments, any criticism of the use of shells from different snail populations because of behavioural differences between snail populations (or behavioural differences between morphs) was overcome.

A random sample of 15 shells of each morph from those used at Site 2 (82 **YU**, 76 **Y5**) was measured from the lip across the widest point (width) and from the apex to the base (height). There was no statistically significant difference between the two morphs for shell width ($t_{(28)} = 1.106$) but the unbanded snail shells were significantly higher than the banded shells ($t_{(28)} = 2.407$, $p<0.05$).

Because of their limited availability, undamaged shells were re-used. To test whether there were any preferences for particular snail shells, each shell was numbered on its underside, close to the shell opening, using yellow enamel paint (No.69, Humbrol, Hull.), and records were kept of which shells were put out in each position in the experimental grid and which were attacked by the birds.

9.2.2 Background and Site

The shell populations were presented on grass lawn at two sites. Site 1 was at the Medical and Biological Sciences Building, University of Southampton, but on a different area of grass from that used in previous experiments. The second site was at 25 Alma Road, Bristol (Site 6 in Chapter 6). Each experimental area was a rectangle, 3m x 5m, marked with metal tent pegs into metre-squares.

9.2.3 Predators

The predators were garden birds. Birds observed feeding at Site 1 were 1 female blackbird (Plate 9.2), 1 robin and 4? starlings. Birds observed feeding at Site 2 were 12+ sparrows, 2 blue tits and 1 male chaffinch.

9.2.4 Procedure

The procedure was similar to that described in Chapter 6 but included a pre-training choice trial, which gave information about any prey preferences that the birds might have possessed (Harvey *et al*., 1975). There is often a clear correlation between morph frequencies in *Cepaea* and habitat; on backgrounds of short grass, yellow unbanded shells predominate (Cain and Sheppard, 1950, 1954; Clarke, 1960; Curry, Arnold and Carter, 1964; Jones, Leith and Rawlings, 1977). If the yellow unbanded shells were less conspicuous (more cryptic) on the grass lawn used in my experiments, it could be predicted that there would be selection against (ie. a preference of the birds for) the yellow banded shells in the pre-training choice tests.

The timetable of the experiments was as follows:

Pre-training choice test: 1 day
Training 1: 3 days
Post-training 1 choice test: 1 day
Training 2: 3 days
Post-training 2 choice test: 1 day

Yellow Five-banded shells were used for the first training period at Site 1, and Yellow Unbanded were used at Site 2.

The experimental populations consisted of equal numbers of the two shell types and were presented at a density of 2 prey/m^2, (which repeated the prey density used for the other training experiments). A computer program was used to determine the random distribution of the prey (a variation of that given in General Appendix A).

The shells were placed in their allocated position (see Chapter 6 for further explanation) and adjusted so that the apex was uppermost.

The distributions were changed after three bouts of feeding. The populations were maintained by repeated replacement of predated shells, usually after every bout of predation. Due to the limited number of shells available for these experiments, undamaged shells were refilled. The numbers of each shell type attacked were recorded. The experimental populations were observed throughout and, where possible, individual sets of data were collected for each species of bird. The choice tests lasted over one day.

TABLE 9.1: Experiment 10 - Numbers of Yellow Unbanded (**YU**) and Yellow Five-banded (**Y5**) *Cepaea hortensis* shells predated from 1:1 populations. Values of G_{adj} for a departure from a 1:1 expectation.

	PRE-TRAINING Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON Y5 Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON YU Numbers taken		$G_{adj(1)}$ (deviation from 1;1)
SITE	YU	Y5			YU	Y5			YU	Y5	
1	32	52	4,78*	→	[34	58	6,30*	→	46	38	0,76]
2	24	37	2,77	→	[31	43	1,94	←	33	33	0,00]

Arrows indicate order of experiment. Asterisks indicate level of statistical significance; *p<0,05.

The training period consisted of placing between 10 and 30 shells of one type over the experimental area. The density of training shells was varied to prevent the birds 'expecting' to find approximately two shells in each metre-square. Each training period lasted for three days. Shells were not left out overnight because of potential predation by nocturnal animals such as rodents and hedgehogs.

The experiment at Site 1 ran from 18th - 28th June 1984, and the experiment at Site 2 ran from 14th - 22nd May 1985.

9.3 RESULTS

Table 9.1 gives the numbers of unbanded and banded shells attacked during the 1:1 presentations. At both sites there was an initial preference for the banded shells as seen from the results of the pre-training experiments, and this trend was statistically significant at Site 1.

At Site 1 the birds were trained first on banded shells. After this training period, during which a total of 501 shells were attacked, a comparison of the deviations from 1:1 ratios shows that the preference for banded increased. The birds were then trained on unbanded shells (312 shells attacked) and this reversed their preference to the extent that they took more unbanded shells.

At Site 2 unbanded shells were used for the first training period (253 shells attacked) and equal numbers of the two shell types were attacked in the subsequent choice test. After training on banded shells (174 shells attacked), relatively more banded shells were again attacked. Although the results at this site were not statistically significant, the changes of preferences were in the predicted directions and follow a similar pattern to that seen at Site 1.

G tests on the data from Site 1 showed that there were significant differences between the proportions of the two shell types attacked in the trials after the two types of training ($G_{adj(1)}$ = 5.592, $p<0.05$) and

TABLE 9.2: Experiment 10 - Numbers of Yellow Unbanded (**YU**) and Yellow Five-banded (**Y5**) *Cepaea hortensis* shells predated from 1:1 populations by one blackbird at Site 1. Values of G_{adj} for a departure from a 1:1 expectation.

PRE-TRAINING Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON Y5 Numbers taken		$G_{adj(1)}$ (deviation from 1;1)		TRAINED ON YU Numbers taken		$G_{adj(1)}$ (deviation from 1;1)
YU	Y5			YU	Y5			YU	Y5	
20	41	7,32**	→	[22	40	5,26*	→	43	37	0,45]

Arrows indicate order of experiment, Asterisks indicate level of statistical significance; *p<0,05, **p<0,01, during the pre-training trial and the **YU**-trained trial ($G_{adj(1)} = 4.671$, $p<0.05$). The deviations in both analyses are in the direction predicted by the hypothesis that the birds choose familiar prey types. There was no significant difference between the proportions taken during the pre-training trial and the **Y5**-trained trial ($G_{adj(1)} = 0.024$), but the direction of the deviation was again in the direction predicted. Although the direction of the changes in the birds' preferences for the prey types was in the predicted direction, the same G tests on the data from Site 2 gave no significant results (**YU**-trained v **Y5**-trained: $G_{adj(1)} = 0.915$; Pre-trained v **YU**-trained: $G_{adj(1)} = 1.442$; Pre-trained v **Y5**-trained: $G_{adj(1)} = 0.089$).

There was no heterogeneity between sites (Pre-trained: $G_{adj(1)} = 0.023$; **Y5**-trained: $G_{adj(1)} = 0.415$; **YU**-trained: $G_{adj(1)} = 0.333$).

Table 9.2 shows the numbers of each shell type taken by the female blackbird at Site 1. This was the only predation that could be attributed to one species of bird. At Site 2 there were usually two or more species feeding at the same time and only very few of the attacks on shells could be scored as predation by particular species. As can be seen in Table 9.2, the blackbird had a strong pre-training preference for the banded shell type and this was not affected by training on this same prey type (comparison of deviations from 1:1 expectation). However, after training on the unbanded shell type, the preference was reversed and this is statistically significant (**YU**-trained v **Y5**-trained: $G_{adj(1)} = 4.69$, $p<0.05$; Pre-trained v **YU**-trained: $G_{adj(1)} = 6.16$, $p<0.02$; Pre-trained v **Y5**-trained: $G_{adj(1)} = 0.10$, N.S.).

9.4 DISCUSSION

This experiment was designed to test further whether wild birds can acquire preferences for familiar prey types that differ in their colour patterns. The results from Site 1 clearly showed that they do, and the results from Site 2 followed a similar trend.

The pre-training choice tests indicated preferences for the banded shells. Many studies of populations of *Cepaea nemoralis* and *C. hortensis* have found correlations between morphs and habitat. Most analyses have been on populations of *C. nemoralis* and have found that on backgrounds of short grass or turf, the yellow unbanded (or effectively unbanded morphs: those with the uppermost band missing) often predominate (Cain and Sheppard, 1950, 1954; Clarke, 1960, 1962; Curry *et al.*, 1964; Jones *et al.*, 1977). Clarke (1960) demonstrated a similar correlation in *C. hortensis*: colonies in grassland have a greater proportion of unbanded yellow shells, those in habitats with dense vegetation or with a dark background colour have a greater proportion of yellow banded shells with the bands fused and those in hedgerows and rough herbage have a greater proportion of unfused banded yellow shells. The backgrounds of lawn at Sites 1 and 2 could have resembled the natural habitat of some populations of *Cepaea* (Harvey *et al.*, 1975), therefore the preferences for the banded snails in the pre-training choice tests could have been because these shells were less cryptic than the unbanded shells. Hypothetically, this visual selection at both sites might have finally resulted in monomorphic populations of unbanded shells unless frequency-dependent selection, in favour of the rarest shell type, stabilised the polymorphism. The post-training choice tests at Site 1 demonstrated behaviour by predators that could lead to apostatic selection. The results from Site 2, although not statistically significant, followed the same trend as those from Site 1.

Many more birds were seen feeding on the prey at Site 2 than were observed at Site 1, and fewer shells were attacked during the training periods at Site 2. This meant that individual birds at Site 2 would have had less experience with the snail shells during the training. Consequently there could have been weaker training responses by the individual birds and this would have led to a weaker overall result. At Site 1 the majority of the predation was by one bird and there was a much clearer result. Another possible important difference between the birds feeding at the two sites was that the birds at Site 2 were unlikely to feed on snails as large as adult *Cepaea* under normal conditions, whereas it is possible that the blackbird at Site 1 could have had previous experience of feeding on snails. The song thrush is not the only thrush that feeds on snails: blackbirds have been observed to do so on occasion (Rooke, 1954; Butlin, 1959; Benson, 1963; Simms, 1978; Tucker, G.M. personal observations at Rogate, Sussex). However, this difference should only have affected their pre-training preferences and their handling of the prey.

Harvey, Birley and Blackstock (1975) performed their training experiments with unbanded brown and yellow *Cepaea nemoralis* shells at two sites. Colour patterns were therefore not involved in their experiments. At each site they presented over a period of three days pre-training populations consisting of equal numbers of the two shell types. The populations were put out at noon each day and left for five hours. A total of thirty-one prey was taken at Site A and a total of twenty-nine was taken at Site B. There were significant preferences for the yellow shells at both sites (Site A: $G_{adj(1)} = 3.926$, $p<0.05$; Site B: $G_{adj(1)} = 4.206$, $p<0.05$). This preference was in the opposite direction from that predicted from studies on *Cepaea* where snails with yellow shell ground colour were the most frequent in populations living on grass (Cain and Sheppard, 1954). The training period lasted over five days and five monomorphic populations of thirty shells were presented at each site during this time. Seventy-one yellow shells were taken at Site A, and seventy-six brown shells were taken at Site B. The post-training period was a repeat of the pre-training period and showed a highly significant change in the proportion of the two shell types taken after training when compared to that taken before training at Site B. There was an increase in the numbers of brown prey taken after training at Site A compared with before training but the totals did not differ significantly from one another ($G_{adj(1)} = 2.77$, $p<0.1$). Although Harvey *et al.* claimed that there was heterogeneity in the post-training results at Site A obtained from comparing each day with the pre-training results, there was no heterogeneity between the results from the three post-training days ($G_{adj(2)} = 5.84$). Unfortunately, the reverse experiments (training on the prey type not used previously) were not carried out, so it cannot be assumed that the birds would have overpredated the familiar prey after a second period of training, as they did in my experiments (although the results from my experiments lead to that prediction). Harvey *et al.* concluded from their experiment that the behaviour demonstrated would lead to frequency-dependent selection that could maintain a shell colour polymorphism in a population where morph frequencies are influenced by thrush predation.

My experiment with snail shells showed that birds could also be trained to search for a particular morph on the basis of the presence or absence of a colour pattern, and it demonstrated behaviour that could lead to the maintenance of a colour pattern polymorphism. The prey density used (2 prey/m^2) was different from that used by Harvey *et al.* (1 prey/4m^2), and this meant that the acquisition of preferences for prey types after training was not a result of the birds' feeding behaviour at any particular density.

The bird species observed feeding in my experiment were different from those in Harvey *et al.*. In their paper they attributed all predation to thrushes; although predation was not observed, they state that "all the shells were accounted for at the end of each day, either untouched or broken by thrushes on stones placed nearby". Thus, as discussed above, behaviour that would lead to frequency-dependent selection has been demonstrated in a variety of different bird species (see also Chapter 6). It would seem that this type of behaviour may be common (in other words, general), and perhaps one can also generalise that many colour-pattern polymorphisms may be maintained by predation.

9.5 SUMMARY

1. This experiment was designed to test further whether wild birds can acquire preferences for familiar prey types that differ in their colour patterns.
2. This experiment was similar in design to that used in Chapter 6 but (following experiments by Harvey, Birley and Blackstock, 1975) it was hoped that by using snail shells as the experimental prey, a more 'natural' experimental design would be achieved than those used previously.
3. *Cepaea hortensis* shells, filled with pastry, were used as the prey. Two morphs were used: Yellow Unbanded and Yellow Five-banded. Snails in general would be familiar, whether or not as potential prey, to most

garden birds and there would be a degree of variation within each group of morphs that was not present in experiments using pastry prey.

4. Wild birds at two sites were presented with pre-training populations of the two shell types to control for any preferences. At both sites there were preferences for the banded shells and this was statistically significant at one site.

5. The birds were then trained on populations of one shell type and then offered a choice between equal numbers of the two shell types. The experiments were then repeated at both sites with the birds being trained on the second shell type.

6. At both sites the familiar shell types were overpredated and at one site this was statistically significant.

7. This experiment demonstrated behaviour that could lead to the maintenance of colour-pattern polymorphism in prey species by their predators. It also extended the work reported in previous chapters and by other authors, and this is discussed.

CHAPTER 10

EXPERIMENTS 9a, 9b & 9c: THE EFFECTS OF PREY FREQUENCY AND DENSITY

10.1 INTRODUCTION

The experiments reported so far on frequency-dependent selection have been 'training experiments', in which birds have been trained on monomorphic prey before being presented with a polymorphic prey population. It has been shown that this training is effective; in that disproportionately more of the familiar prey type is usually taken.

The absolute density of the prey has been shown to have an effect on the magnitude of frequency-dependent selection, its direction (i.e. whether rare or common forms are at an advantage) and also on whether frequency-dependent selection occurs at all (Allen, 1972; Cook and Miller, 1977; Horsley, Lynch, Greenwood, Hardman and Mosely, 1979; Willis, McEwan, Greenwood and Elton, 1980; Allen and Anderson, 1984). At relatively high densities it appears to be anti-apostatic, the result of which would be monomorphism; and at lower densities where more active searching would take place there is evidence for apostatic selection, which could result in the maintenance of polymorphism. However, there appear to be significant differences in the results obtained by different workers, much of which have been put down to individual differences between birds or between species of birds. In experiments where, although the prey density was not at maximum, it might be presumed that most of the prey were within detection-distance, chicks either exhibited apostatic selection (Fullick and Greenwood, 1979) or no frequency-dependent selection (Willis *et al.*, 1980). At a prey density of $9/m^2$ (Cooper, 1984b) wild passerine birds preyed apostatically. Experiments with contiguous prey have, on the whole, found predation to be anti-apostatic (Allen, 1972; Horsley *et al.*, 1979; Allen and Anderson, 1984) although experiments by Harvey, Jordan and Allen (1974) resulted in apostatic selection. Little work has been done at very low densities; it might be that, at very low prey densities, there would be no frequency-dependent selection since times between prey capture would be relatively long and a predator might not be behaving optimally if it rejected any prey type that it came across (Clarke, 1962).

In order to study the effects of prey density on frequency-dependent selection a range of prey frequencies as well a range of prey densities are usually used, instead of training experiments, because this allows statistical analysis using the methods of Manly (1974) and Elton and Greenwood (1970). These methods would give regression lines which can be directly compared both between densities and between frequencies. This design also counters any criticisms of the interpretation of the results from training experiments as evidence for frequency-dependent selection (eg., Greenwood and Elton, 1979; Greenwood, 1985; see Chapter 11 for further discussion).

The prey density used in the training experiments reported in Chapters 6, 7 and 9, was 2 prey/m^2; the density used in the chick training experiment in Chapter 8 was 30 prey/m^2; and the densities used in the choice tests (Chapters 3, 4 and 5) were 30 prey/m^2 and 1 prey/4m^2. These three prey densities plus a 'maximum' prey density of 3850 prey/m^2 were used in the series of experiments reported in the present chapter. The densities ranged from one in which the prey formed a continuous mass, through one in which the predator could see most of the prey from a single vantage point, and where the predator could see only a few of the available prey at any one time, to one in which the inter-prey distances meant that only one prey could be seen by the predator (when on the ground).

There were three series of experiments using plain and striped pastry prey. Experiment 9a gave the birds a range of prey frequencies at the density of 30 prey/m^2; Experiment 9b repeated the design of Experiment 9a at the prey density of 3850/m^2 (contiguous prey); Experiment 9c changed both the prey frequency and prey density in a random order and all four prey densities described above were used.

By using this range of densities and a range of prey frequencies, it was hoped to examine frequency-dependent selection on plain and striped colour patterns in prey that are similar in colour to their backgrounds. Experiments of this type have not been done before with

TABLE 10.1: Sites, map references and chronology for Experiments 9a, 9b and 9c.

EXPERIMENT	SITE	ADDRESS	MAP REFERENCE	CHRONOLOGY
9a	1	25 Alma Rd Bristol	ST 575739	17 Apr - 27 Apr 1984
	2	10 Richmond Gdns Southampton	SU 430145	4 Jun - 14 Jun 1984
9b	1	25 Alma Rd Bristol	ST 575739	2 Jul - 15 Jul 1984
	2	8 Kings Rd Chandlers Ford	SU 435210	24 Jul - 2 Aug 1984
9c		Boldrewood Southampton	SU 418156	2 May - 25 May 1984

TABLE 10.2: Experiments 9a, 9b and 9c - species of birds observed feeding at each site. For scientific names see Table 2.1.

EXPERIMENT	9a		9b		9c
SITE	1	2	1	2	
House sparrow	+	+	+	+	-
Blackbird	+	(+)	+	+	(+)
Starling	+	-	-	+	+
Chaffinch	+	(+)	-	-	(+)

(+) indicates the presence of that species of bird but that it contributed very little to the total number of prey eaten.

striped/plain prey types and only Cooper (1984b) has done similar experiments with prey that matched their backgrounds.

10.2 MATERIALS AND METHODS

10.2.1 Prey

The prey were two of the prey types described in Chapter 2 and had been used in previous experiments: plain green (**G**) and green with a red stripe (**GR**). (Plate 4.1, Chapter 4.)

10.2.2 Backgrounds and Sites

The prey populations were presented on grass lawns at two sites in Experiment 9a, at two sites in Experiment 9b, and at one site in Experiment 9c. One site was common to both Experiment 9a and Experiment 9b. Table 10.1 gives the Ordnance Survey map references for each site and the chronology of the experiments.

Each experimental area in Experiment 9a was a rectangle 1m x 2m that was marked out into two 1m x 1m squares with metal tent pegs. The experimental areas in Experiment 9b were the areas covered by the total prey population and were not marked out on the lawn. The experimental area in Experiment 9c varied depending on the density of prey used at any one time. Metal tent pegs were used to mark out metre-squares for the relevant trials.

10.2.3 Predators

Wild garden birds were again the predators. Table 10.2 lists the species of birds observed feeding at each site.

10.2.4 Procedure

a) Experiment 9a

The prey density for these experiments was 30 prey/m^2. Five prey frequencies (1:9, 3:7, 5:5, 7:3, 9:1) were used at Site 1 and seven prey frequencies (1:9, 2:8, 3:7, 5:5, 7:3, 8:2, 9:1) were used at Site 2. These were presented in a random order with the exception that the frequency 5:5 was presented first at both sites to act as controls for

PLATE 10.1: Example of 'maximum' density population (3850/m^2). Prey frequency is 7GR:3G.

any pre-experimental preferences. Each experiment at a particular prey frequency consisted of five successive trials, except for the 5:5 series of trials at Site 1 when the very fast predation was taken advantage of and ten replicates were achieved. One day was allowed for each series of trials at each frequency. At the start of each trial, 30 prey (in the appropriate proportions) were placed in each of the two metre-squares by dropping them from waist-height. The prey were placed so that they did not overlap and so that their colour pattern was uppermost. The experimental populations were observed and, where possible, individual sets of data were collected for each species of bird. The birds were allowed to feed until approximately half of the prey had been eaten (following Manly, Miller and Cook, 1972) so that statistical comparisons between trials could be made from data obtained at approximately the same point in each trial; and then the numbers of each prey type eaten were recorded. There was no prey replacement during a trial.

b) Experiment 9b

The procedure for these experiments was essentially the same as that for Experiment 9a except that the prey were placed at their maximum density - as close together as possible without them overlapping each other (Plate 10.1). This resulted in a density of approximately 3850 prey/m^2. The prey population size was 60. Five prey frequencies (1:9, 3:7, 5:5, 7:3, 9:1) were used at each site. The first experimental prey frequency at both sites was 5:5 in order to test for any preferences by the birds for either prey type.

c) Experiment 9c

In this experiment both prey density and prey frequency were changed and the order in which the different prey densities and frequencies were presented was random. There were five frequencies (1:9, 3:7, 5:5, 7:3, 9:1) and four densities (3850 prey/m^2, 30 prey/m^2, 2 prey/m^2, 1 prey/4m^2). The prey population size for the first three densities was 60 prey, and, because of practical reasons related to the size of the experimental area, the population size for the lowest density was 30 prey. As in the other two experiments, there were five successive trials at each frequency. The procedure for the presentation of each population at the two higher densities was as described above for Experiments 9a and 9b. A modified version of the computer program

TABLE 10.3: **Experiments 9a, 9b and 9c** - the prey frequency/density presentation orders.

EXPERIMENT	9a		9b		9c	
SITE	1	2	1	2		
DAY	**GR:G**	**GR:G**	**GR:G**	**GR:G**	**Prey/m^2**	**GR:G**
1	5:5	5:5	5:5	5:5	30/m^2	3:7
2	3:7	2:8	7:3	9:1	1/4m^2	7:3
3	9:1	1:9	1:9	3:7	30/m^2	9:1
4	7:3	9:1	3:7	7:3	3850/m^2	3:7
5	1:9	7:3	9:1	1:9	3850/m^2	9:1
6		8:2			2/m^2	9:1
7		3:7			3850/m^2	5:5
8					30/m^2	5:5
9					3850/m^2	1:9
10					2/m^2	3:7
11					1/4m^2	3:7
12					1/4m^2	9:1
13					1/4m^2	1:9
14					30/m^2	7:3
15					2/m^2	1:9
16					30/m^2	1:9
17					2/m^2	7:3
18					1/4m^2	5:5
19					3850/m^2	7:3
20					2/m^2	5:5

mentioned in previous chapters was used to decide the prey distributions at the two lower densities (General Appendix A). As in Experiments 9a and 9b, the experimental populations were observed and, when possible, predation by individual bird species was recorded. Predation was halted when approximately half the prey had been eaten and the numbers of each prey type taken were recorded.

The orders of the presentation of the prey frequencies at each site for each Experiment are shown in Table 10.3.

10.2.5 Statistical Analysis

A series of selection coefficients against **GR** (β of Manly, 1973, 1974) were calculated. β measures the probability that the next prey to be taken will be **GR** if the two prey types were presented at the ratio 1:1, and varies from 0 to 1, with the value of 0.5 indicating no selection. The β values were subjected to arcsin transformation to permit parametric statistical analysis. Thus the transformed values of β (β_T) ranges from 0 to 90 and a value of 45 indicates no selection. A value of more than 45 indicates selection against **GR** prey, and a value of less than 45 indicates selection against **G** prey. To test for the effect of frequency, β_T was plotted against the frequency of **GR** prey available and regression analysis was performed. If the slope of the regression line departs from zero then frequency-dependent selection is indicated: a positive slope means apostatic selection and a negative one means anti-apostatic. The steeper the slope, the greater the selection.

The β coefficient of Manly (1973, 1974) has been criticised by Greenwood and Elton (eg., 1979) because of the assumption that β remains constant during the course of a trial. The model assumes that the predator knows, right from the start of the experiment, the frequencies of the prey types and proceeds to feed with a correspondingly adjusted β value, a value that is unaffected by either changes in the relative prey frequencies or by any learning response by the predator. If predators have to learn to select in a frequency-dependent manner, then β will be expected to change throughout the trial. Thus the assumption that β remains constant throughout a trial seems unlikely. However, the general conclusions drawn from using this model are unlikely to be incorrect and other workers have shown that Manly's model can be successfully fitted to various data (Greenwood and Elton, 1979).

Greenwood and Elton (1979) and Elton and Greenwood (1970) have suggested an alternative model where the outcome of a selection experiment may be described by the relationship $e_1/e_2 = (VA_1/A_2)^b$, where e_1 and e_2 are the numbers of the two forms eaten, A_1 and A_2 are the numbers available, V is a measure of frequency-independent selection and b is a measure of frequency-dependent selection. If b is greater than 1, selection is apostatic: if b is less than 1, selection is anti-apostatic. The value of b is likely to vary between different predators and different prey and between different experiments. For example, an experiment in which few prey are eaten may allow less learning than one in which more are eaten and the b value may be smaller even if the strength and form of the learning process are the same. This model is descriptive of the outcome of a series of trials in which the ratio A_1/A_2 has been varied, and at the points at which they have been stopped. The model fits published data well (Fullick and Greenwood, 1979; Greenwood and Elton, 1979). A misheld conception about this model is that it can only be used for experiments in which the relative prey densities are kept constant by the replacement of eaten prey (Manly, 1973). Greenwood and Elton (1979) point out that, if selection is frequency-dependent, one would obtain larger (and therefore more statistically significant) values of b if the relative prey densities were kept constant than if they were allowed to change. However, the value of b would still be comparable between experiments of similar design. Therefore, one would not be drawing the wrong conclusions from an experiment in which there was no replacement but statistically significant results would be more difficult to obtain.

Using this model, the values of e_1/e_2 were plotted against A_1/A_2 after transforming both ratios to logs, and estimates of b and V were obtained using regression analysis.

The data obtained from the series of experiments reported in this chapter was analysed using both the above methods. This allows a comparison between the two methods and helps allay any criticisms of the use of either method.

10.3 RESULTS

The raw data are given in the appendix to this chapter.

Figures 10.1 - 10.8 show the results from Experiments 9a, 9b and 9c graphically. For each of the sites in Experiments 9a and 9b and for each density in Experiment 9c there are three graphs.

Graphs A of each figure give the proportion of **GR** prey eaten plotted against the proportion of **GR** prey available. A sigmoidal distribution would indicate the presence of apostatic or anti-apostatic selection.

Graphs B of each figure give β_T for **GR** prey plotted against the proportion of **GR** prey available. The regression line was fitted by linear regression analysis (Sokal and Rholf, 1981). If the gradient of the line departs from zero apostatic selection is indicated if the gradient is positive and anti-apostatic selection if the gradient is negative. The gradient represents the intensity of the selection: the steeper the slope the stronger the selection. The point where the regression line crosses the line of random predation (represented by a broken line) shows the level of frequency-independent selection (any frequency-independent preference for either prey type). If the regression line crosses the line of random predation at 0.5 then there is no frequency-independent selection; if it crosses at a point on the line higher than 0.5 then there is a frequency-independent preference for **GR** prey, and the reverse is the case if the point is lower than 0.5.

Graphs C of each figure show the results analysed by the methods of Greenwood and Elton (1979). The logarithm of the number of **GR** prey eaten divided by the number of **G** prey eaten is plotted against the logarithm of the number of **GR** prey available divided by the number of **G** prey available. A regression line is fitted. A gradient that differs from unity indicates frequency-dependent selection: greater than unity represents apostatic selection, less than unity represents anti-apostatic selection. The value 'V' in the selection equation of Greenwood and Elton (1979) is a measure of frequency-independent selection and can be calculated using values obtained by regression analysis. If its value is

TABLE 10.4: Experiment 9a - Equations of regression lines in Figures 10.1B and 10.2B (analysis following method of Manly, 1973) with the values of t for the departure of the observed gradient from zero.

SITE	EQUATION OF LINE	t	df	p
1	$y = 58.233 - 1.863x$	3.345	28	<0.01
2	$y = 49.475 - 1.064x$	3.965	33	<0.001

TABLE 10.5: Experiment 9a - Equations of regression lines in Figures 10.1C and 10.2C (analysis following method of Greenwood and Elton, 1979), estimated V values and values of t for the departure of the observed gradient from unity.

SITE	EQUATION OF LINE	V	t	df	p
1	$y = 0.082 + 0.854x$	1.247	2.481	23	<0.05
2	$y = 0.901x - 0.018$	0.955	3.940	33	<0.001

unity, there is no frequency-independent selection. If its value is greater or less than unity, there is frequency-independent selection for one or other of the prey types. The points at which the regression line crosses the x and y axes also represent frequency-independent selection; values close to zero indicate frequency-dependent selection is almost absent.

10.3.1 Experiment 9a (30 prey/m^2) - Figures 10.1 and 10.2

The graphs show that selection was anti-apostatic. There is a sigmoidal distribution in Figures 10.1A and 10.2A in which the proportion of prey eaten is plotted against the proportion of prey offered. Analysis of variance on the β_Ts obtained show statistically significant differences between frequencies (Site 1: $F_{(4,25)} = 4.155$, $p<0.05$; Site 2: $F_{(6,28)} = 3.612$, $p<0.01$), and further analysis indicates linear regression (Site 1: $F_{(1,3)} = 7.529$, $p<0.1$; Site 2: $F_{(1,5)} = 14.217$, $p<0.025$). Figures 10.1B and 10.2B show the regression lines, both of which have negative slopes. In each case, these slopes are statistically significantly different from zero, indicating frequency-dependent selection. The two slopes do not differ significantly from one another ($F_{(1,8)} = 1.540$). Table 10.4 summarises the analysis.

Analysis using the method of Greenwood and Elton (1979), and shown in Figures 10.1C and 10.2C, also shows that selection was anti-apostatic, with both regression slopes having gradients significantly less than unity. The statistical analysis is summarised in Table 10.5. As in the analysis of β_T, the two regression lines do not differ significantly from each other ($F_{(1,8)} = 0.476$). The degree of frequency-dependent selection, as well as its direction, was similar at both sites.

At Site 1, the regression line for β_T on frequency cut the random predation line at x = 0.711 (Figure 10.1B) and the estimated V value (Table 10.5) is 1.247. Both these values indicate an element of frequency-independent selection against the **GR** prey type. At Site 2, the regression line of Figure 10.2B cut the line of random predation at x = 0.421 and the estimated V value (Table 10.5) is 0.955, indicating a very slight preference for the **G** prey type.

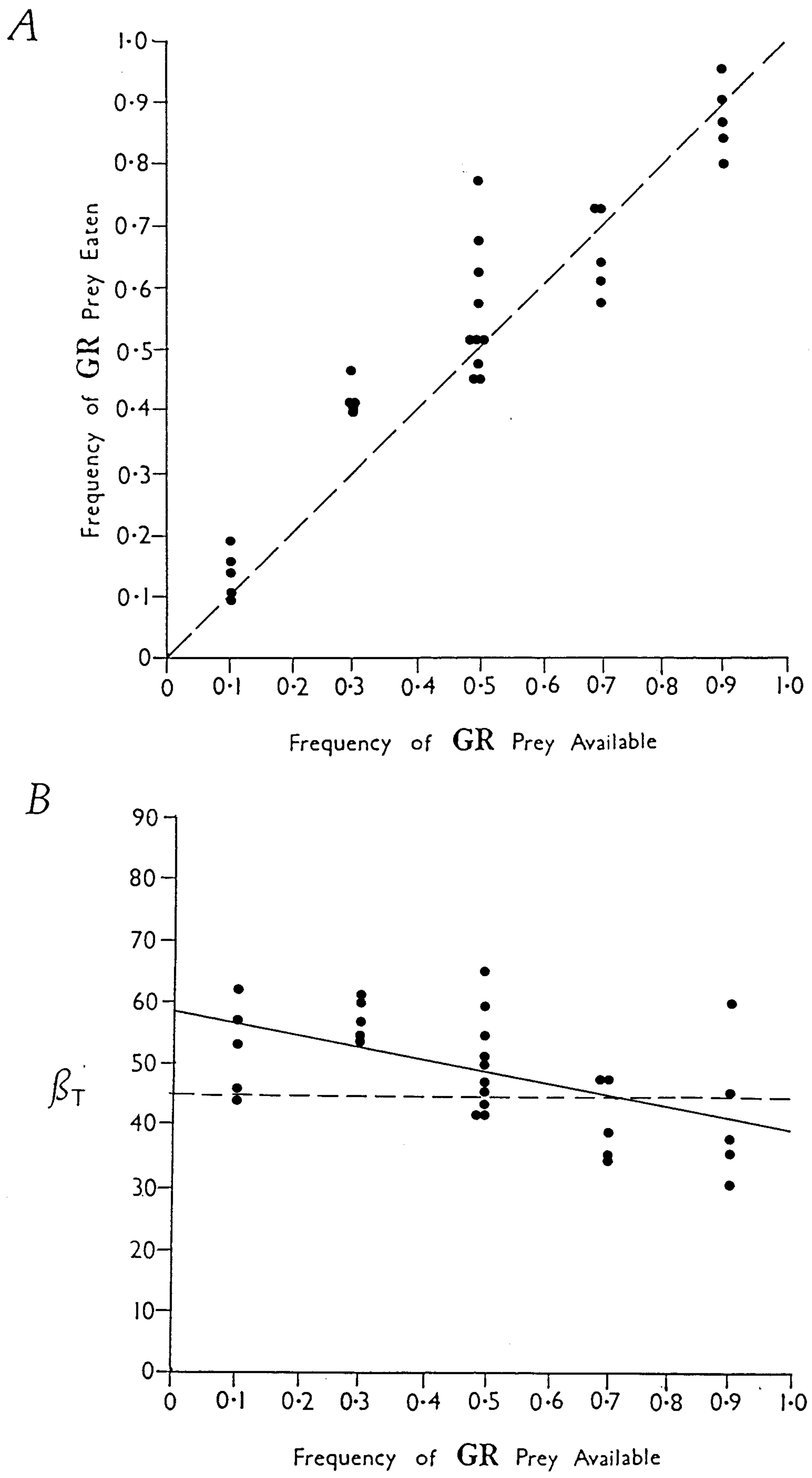
FIGURES 10.1 and 10.2: Experiment 9a.
Frequency-dependent selection at Site 1 (Figure 10.1) and Site 2 (Figure 10.2).

Figures 10.1A and 10.2A: Frequency of **GR** prey eaten plotted against frequency of **GR** prey available. Broken lines represent expected relationship if prey were eaten in the proportions in which they were presented.

Figures 10.1B and 10.2B: β_T (selection against **GR**) plotted against frequency of **GR** prey available. Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Manly, 1973.)

Figures 10.1C and 10.2C: $\text{Log}(e_1/e_2)$ (where e_1 and e_2 are the numbers of **GR** and **G** prey eaten) plotted against $\text{Log}(A_1/A_2)$ (where A_1 and A_2 are the numbers of **GR** and **G** prey available). Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Greenwood and Elton, 1979.)

FIGURE 10.1: Experiment 9a, Site 1. 30 prey/m^2.



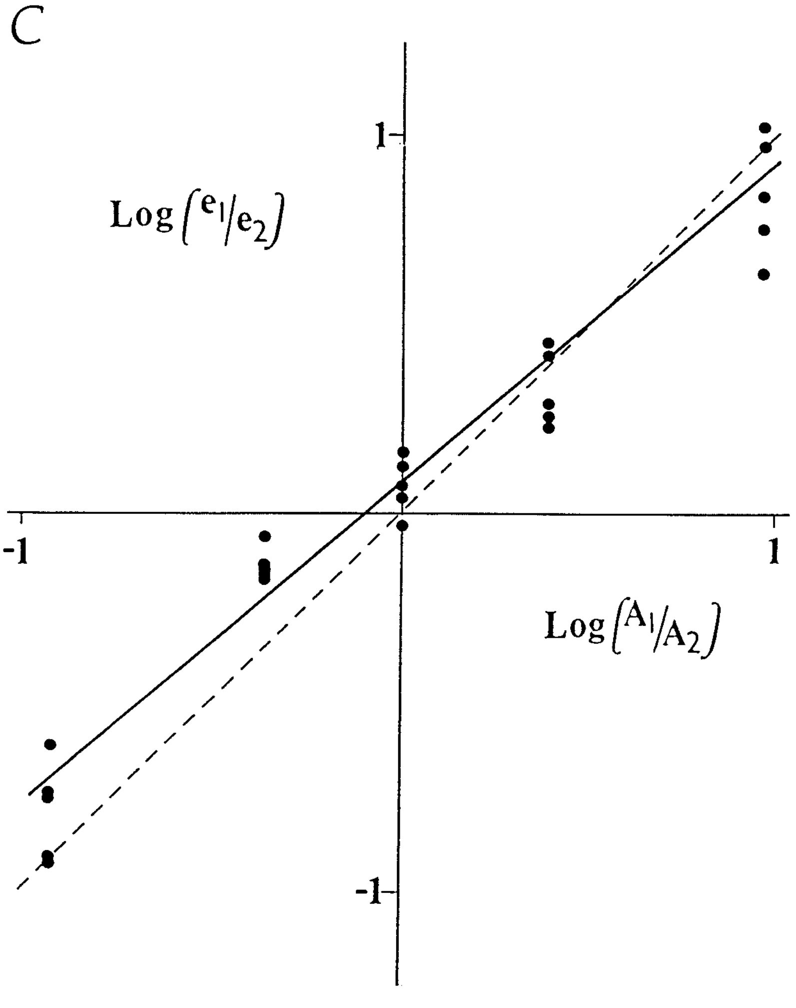
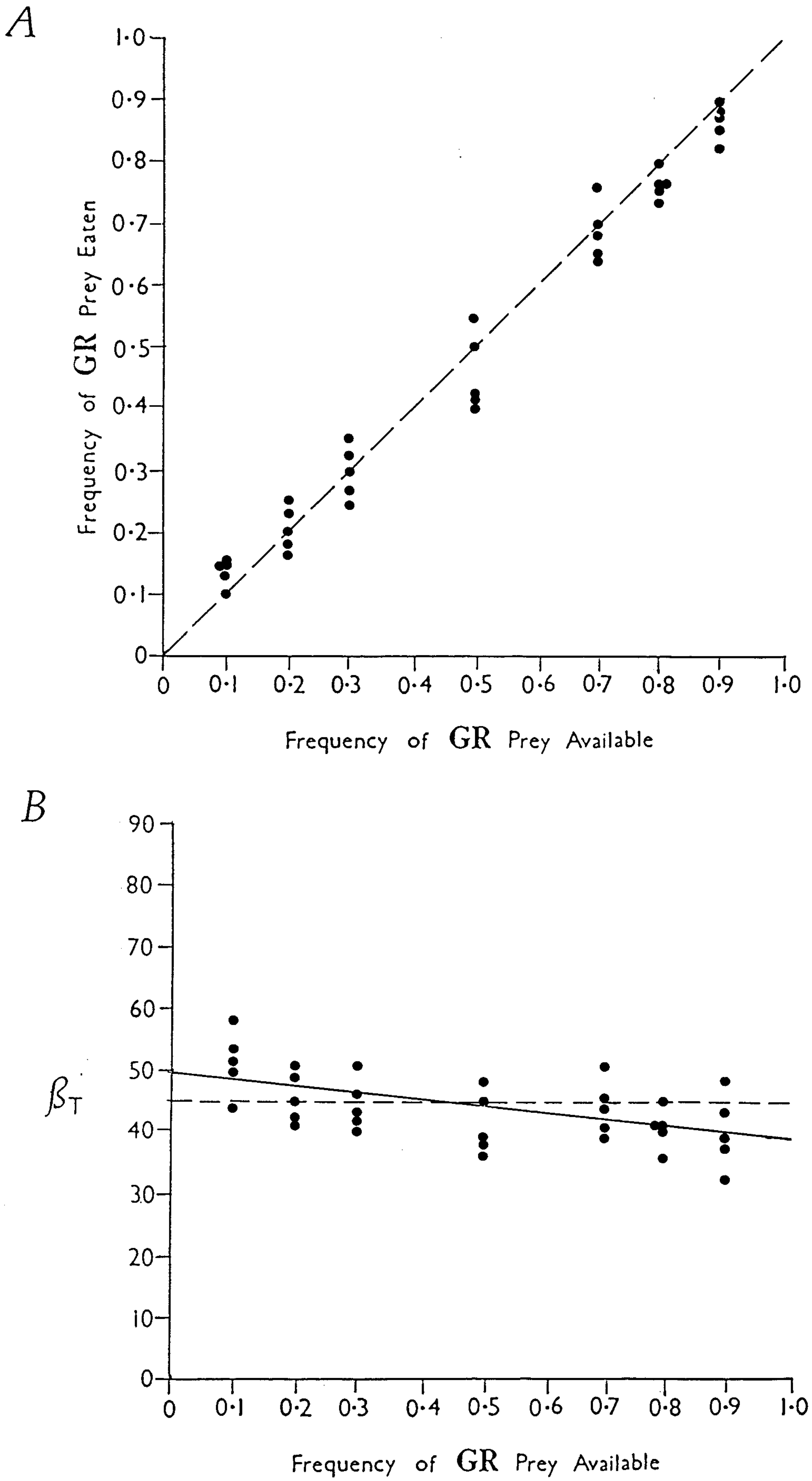

C
Log (e1/e2)
Log (A1/A2)
1
-1
-1
1

FIGURE 10.2: Experiment 9a, Site 2. 30 prey/m^2.



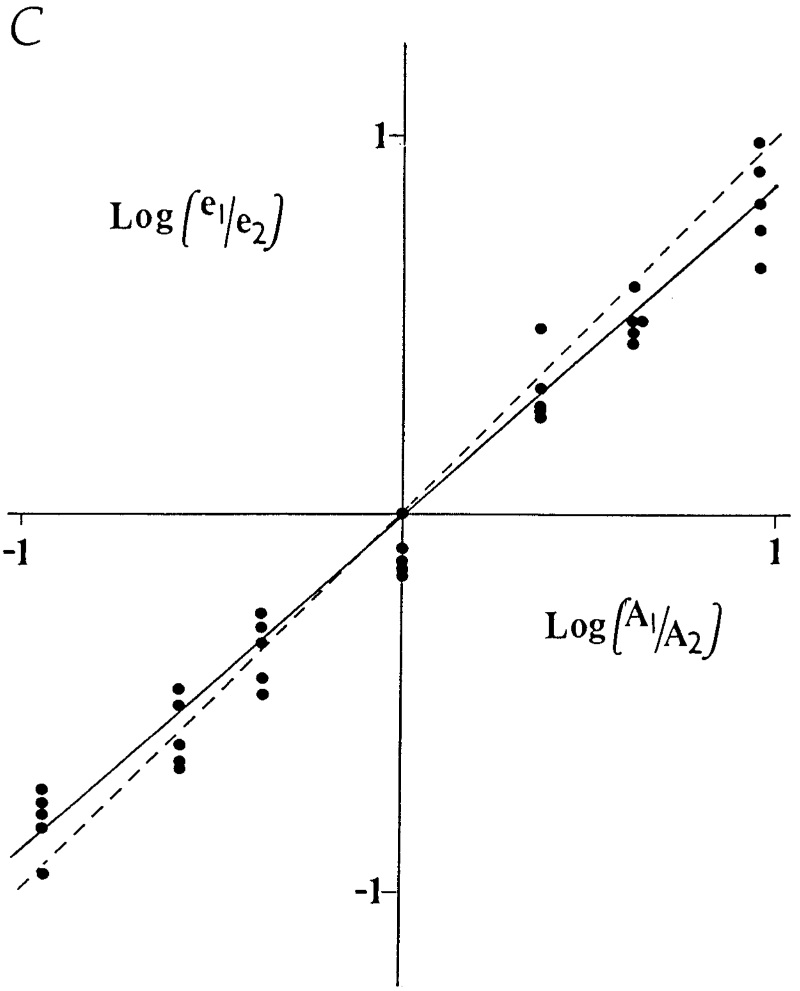

C
Log (e₁/e₂)
1
-1
-1
1
Log (A₁/A₂)

TABLE 10.6: **Experiment 9b** - Equations of regression lines in Figures 10.3B and 10.4B (analysis following Manly, 1973) with the values of t for the departure of the observed slope from zero.

SITE	EQUATION OF LINE	t	df	p
1	$y = 29.785 + 2.152x$	2.340	23	<0.05
2	$y = 47.050 - 0.171x$	0.388	23	N.S.

TABLE 10.7: **Experiment 9b** - Equations of regression lines in Figures 10.3C and 10.4C (Analysis following Greenwood and Elton, 1979), estimated V values and values of t for the departure of the observed gradient from unity.

SITE	EQUATION OF LINE	V	t	df	p
1	$y = 0.060 + 1.106x$	1.133	1.980	3	N.S.
2	$y = 0.025 + 0.990x$	1.060	0.249	23	N.S.

Further information about the frequency-independent selection component is provided by the data from the 5:5 populations, the first frequency used in the experiment. At Site 1, ten trials were carried out at the 5:5 frequency, and G tests on the actual numbers of prey types taken show that there was a statistically significant preference for the **GR** prey type when the numbers of each prey type taken were totalled ($G_{F(1)} = 4.636$, $p<0.05$), although there were no overall preferences when the trials were not totalled ($G_{T(10)} = 14.747$). There was little heterogeneity between trials ($G_{H(9)} = 10.111$, N.S.). There were no detectable preferences found at Site 2 ($G_{T(5)} = 2.365$; $G_{F(1)} = 0.925$; $G_{H(4)} = 1.440$).

10.3.2 Experiment 9b (3850 prey/m^2) - Figures 10.3 and 10.4

Selection at Site 1 was apostatic. Figure 10.3A has a distribution that is basically sigmoidal. Analysis on the β_Ts gives some evidence for differences between frequencies ($F_{(4,20)} = 2.709$, $p<0.1$). Although analysis of variance indicates that there is no evidence for linear regression ($F_{(1,3)} = 3.975$), if a regression line is fitted there is a significantly positive slope (Figure 10.3B). The regression analysis is summarised in Table 10.6.

Because there were zeros in the data from Site 1, the numbers of each prey type taken at each frequency were totalled (following the suggestion of Greenwood and Elton, 1979) for analysis, using the method of Greenwood and Elton (1979). This resulted in the five points on the graph shown in Figure 10.3C. The regression line has a gradient greater than unity, thus indicating apostatic selection; however, this slope is not statistically significant (Table 10.7).

At Site 1, the regression line in Figure 10.3B crosses the line of random predation at the prey frequency of 0.707 (approximately the same point that is cut by the regression line in Figure 10.1B from the same site - Site 1, Experiment 9a). The estimated value of V is 1.133 (Table 10.7). Both these results suggest a preference for the **GR** prey type. However, at the prey frequency of 5:5, there was no preference for either prey type ($G_{T(5)} = 2.529$; $G_{F(1)} = 0.000$; $G_{H(4)} = 2.529$).

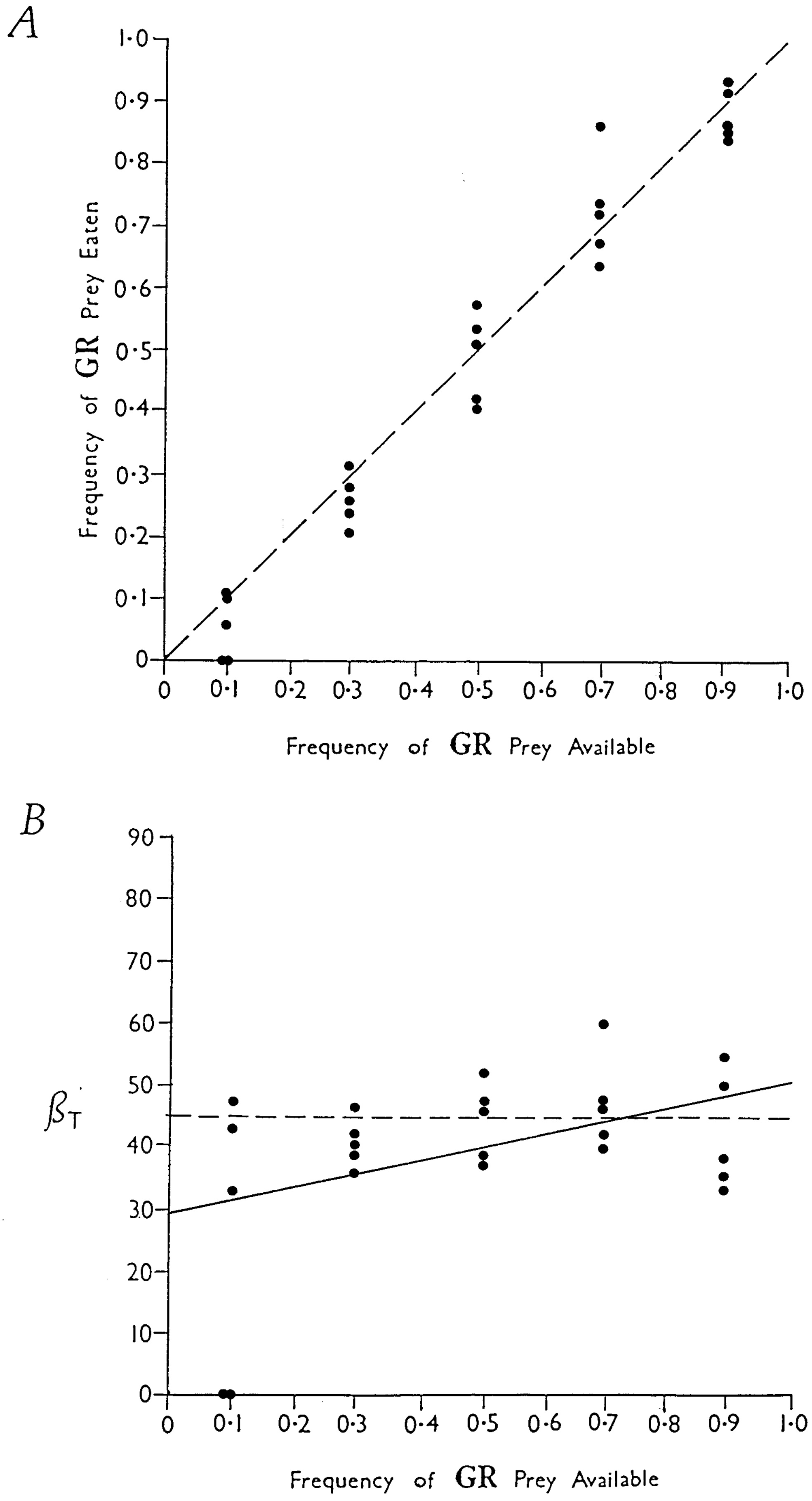
FIGURES 10.3 and 10.4: Experiment 9b.
Frequency-dependent selection at Site 1 (Figure 10.3) and Site 2 (Figure 10.4).

Figures 10.3A and 10.4A: Frequency of **GR** prey eaten plotted against frequency of **GR** prey available. Broken lines represent expected relationship if prey were eaten in the proportions in which they were presented.

Figures 10.3B and 10.4B: β_T (selection against **GR**) plotted against frequency of **GR** prey available. Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Manly, 1973.)

Figures 10.3C and 10.4C: $\mathrm{Log}(e_1/e_2)$ (Figure 10.4C) or $\mathrm{Log}(\Sigma e_1/\Sigma e_2)$ (Figure 10.3C) (where e_1 and e_2 are the numbers of **GR** and **G** prey eaten) plotted against $\mathrm{Log}(A_1/A_2)$ (where A_1 and A_2 are the numbers of **GR** and **G** prey available). Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Greenwood and Elton, 1979.)

FIGURE 10.3: Experiment 9b, Site 1. 3850 prey/m^2.



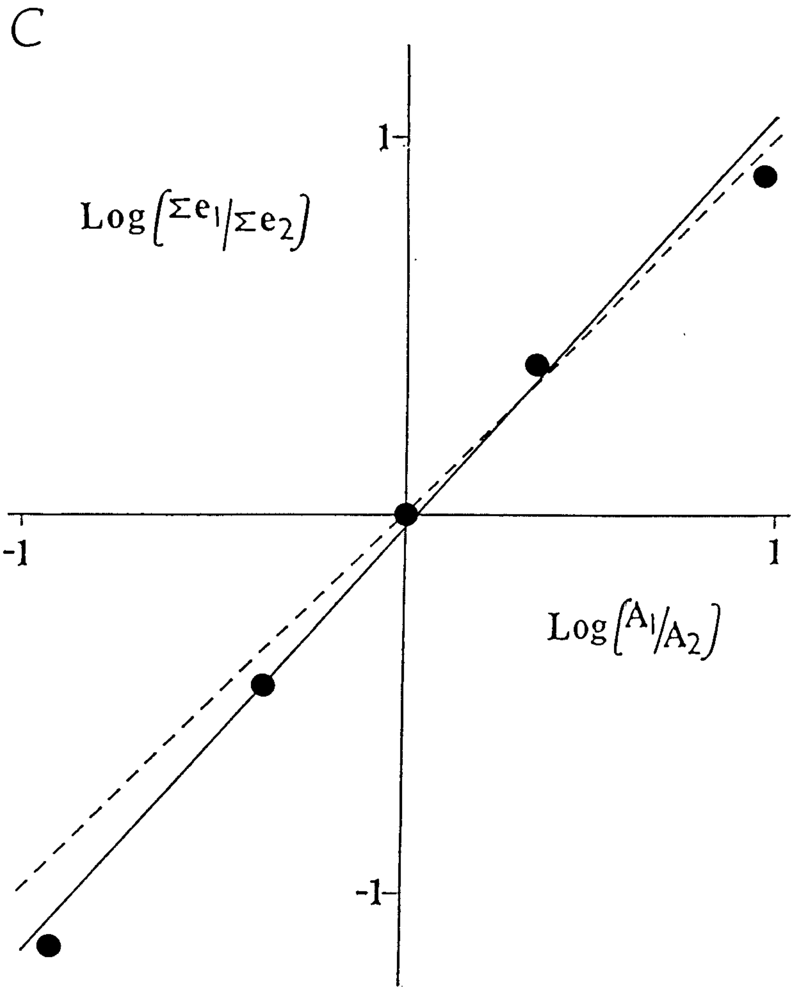
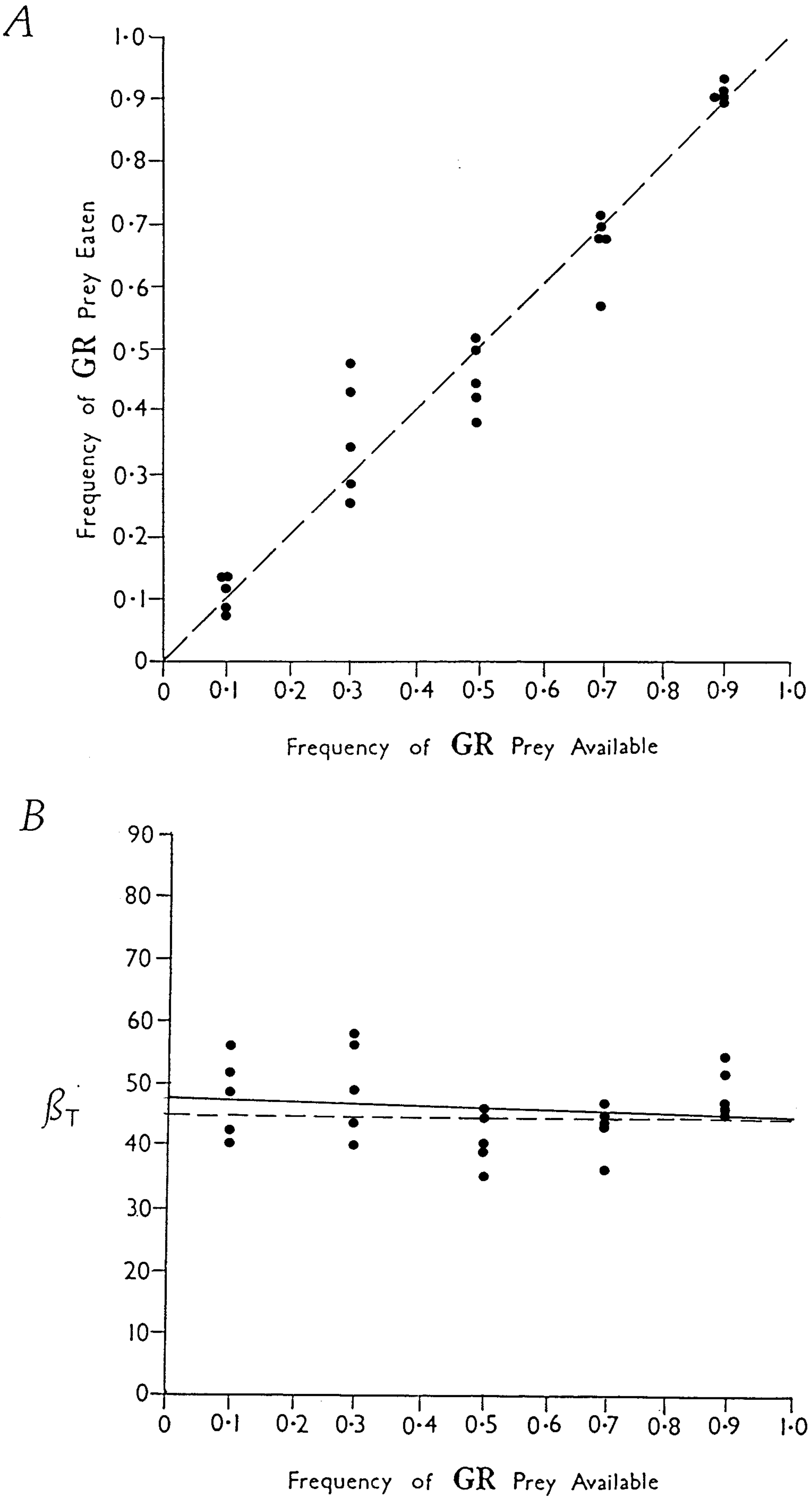

C
1
-1
$\mathrm{Log}(\Sigma e_1/\Sigma e_2)$
-1
1
$\mathrm{Log}(A_1/A_2)$

FIGURE 10.4: Experiment 9b, Site 2. 3850 prey/m^2.



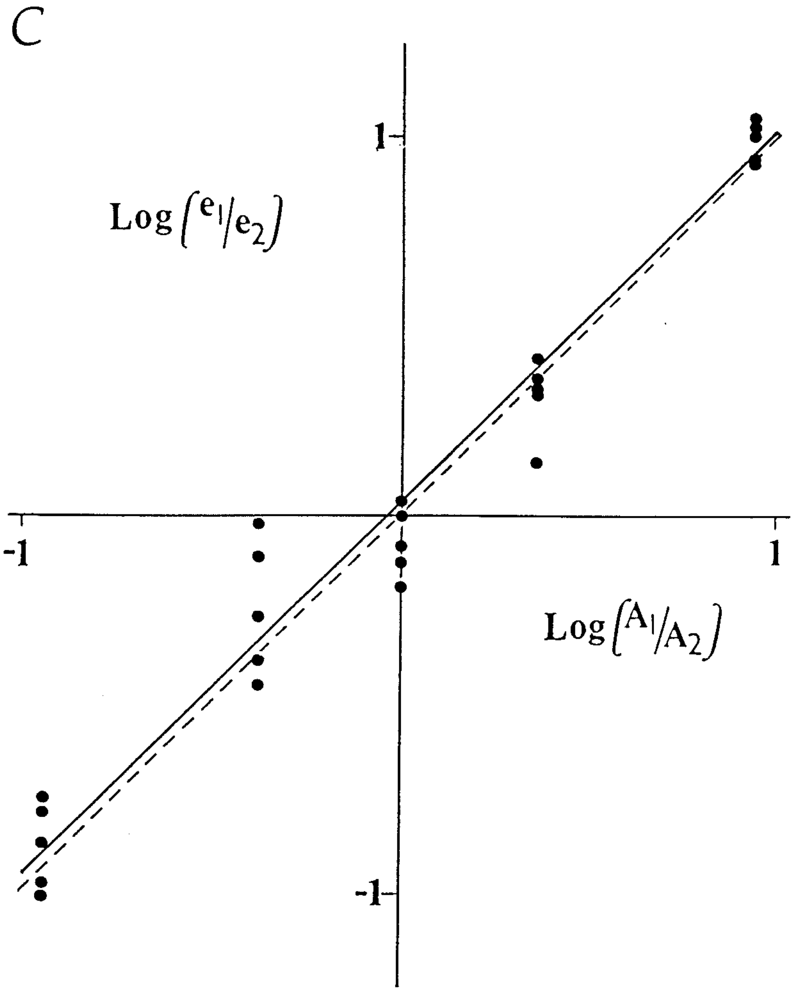

C
1
Log (e1/e2)
-1
1
Log (A1/A2)
-1

TABLE 10.8: Experiment 9c - Two-way analysis of variance table for the effects of density and frequency.

SOURCE	df	SS	MS	F	p
DENSITIES	3	845.49	281.83	2.444	<0.1
FREQUENCIES	4	425.77	106.44	0.923	N.S.
INTERACTION	12	1360.49	113.37	0.983	N.S.
ERROR	80	9225.29	115.32		
TOTAL	99	11857.04			

The results from Site 2 indicate only a very slight anti-apostatic selection. If Figure 10.4A is examined, a sigmoidal distribution is not apparent. There are no significant differences between the β_Ts obtained at each frequency ($F_{(4,20)} = 2.233$) and no significant linear regression ($F_{(1,3)} = 0.065$). The regression line has a very shallow slope that is not significantly different from zero (Table 10.6).

The regression line shown on the graph in Figure 10.4C has a slope that is less than unity but the deviation is not statistically significant (Table 10.7).

Frequency-independent selection against the **GR** prey type is strongly indicated by the point at which the regression line 'cuts' the line of random selection in Figure 10.6: $x = 1.751$. (Since the maximum value of x is unity this is an impossible value and shows one of the criticisms of analysis using Manly's β.) However, the estimated value of V (1.060, Table 10.7) and the data from the frequency of 5:5, indicate no significant preferences for either prey type ($G_{T(5)} = 2.490$; $G_{P(1)} = 1.254$; $G_{H(4)} = 1.236$).

The slopes of the regression lines obtained at Sites 1 and 2 do not differ significantly from each other, even though, in direction, they indicate the opposite forms of frequency-dependent selection (Figures 10.3B and 10.4B: $F_{(1,6)} = 3.338$; Figures 10.3C and 10.4C: $F_{(1,6)} = 0.940$).

10.3.3 Experiment 9c (4 prey densities) - Figures 10.5, 10.6, 10.7 and 10.8

The results from this experiment do not give any real indication of frequency-dependent selection.

Two-way analysis of variance on all the β_Ts obtained from the experiment (Table 10.8) suggests that there is some evidence of differences in prey selection between densities. There is no evidence that there is any frequency-dependent selection from this analysis, and

TABLE 10.9: Experiment 9c - Equations of regression lines in Figures 10.5B, 10.6B, 10.7B and 10.8B (analysis following Manly, 1973) with the values of t for the departure of the observed slope from zero.

DENSITY	EQUATION OF LINE	t	df	p
3850/m^2	$y = 46.870 + 0.847x$	1.037	23	N.S.
30/m^2	$y = 50.571 - 0.785x$	1.703	23	N.S.
2/m^2	$y = 42.429 + 0.145x$	0.279	23	N.S.
1/4m^2	$y = 41.560 + 1.412x$	1.349	23	N.S.

TABLE 10.10: Experiment 9c - Equations of regression lines in Figures 10.5C, 10.6C, 10.7C and 10.8C (analysis following Greenwood and Elton, 1979), estimated V values and values of t for the departure of the observed gradient from unity.

DENSITY	EQUATION OF LINE	V	t	df	p
3850/m^2	$y = 0.043 + 0.947x$	1.111	0.914	3	N.S.
30/m^2	$y = 0.036 + 0.945x$	1.091	1.195	23	N.S.
2/m^2	$y = 0.040 + 1.034x$	1.094	0.772	23	N.S.
1/4m^2	$y = 0.012 + 0.986x$	1.028	0.681	3	N.S.

there is no interaction between density and frequency. The relationship between density and frequency will be examined graphically.

At all densities, there were no preferences for either prey type at the 5:5 frequency (3850/m^2: $G_{T(5)}$ = 0.195, $G_{F(1)}$ = 0, $G_{H(4)}$ = 0.198; 30/m^2: $G_{T(5)}$ = 1.721, $G_{F(1)}$ = 0.390, $G_{H(4)}$ = 1.331; 2/m^2: $G_{T(5)}$ = 4.076, $G_{F(1)}$ = 0.686, $G_{H(4)}$ = 3.391; 1/4m^2: $G_{T(5)}$ = 0.949, $G_{F(1)}$ = 0.131, $G_{H(4)}$ = 0.819). The frequency-independent selection indicated by the values of V greater than unity, obtained using the method of analysis of Greenwood and Elton (1979), show a slight preference for the GR prey type at all four densities (Table 10.10).

Figure 10.5 represents graphically the results from the trials carried out at the 'maximum' density (3850 prey/m^2). In Figure 10.5A there is no evidence of a sigmoidal relationship. Figure 10.5B has a positive regression line (Table 10.9) but neither are there no statistically significant differences between the frequencies ($F_{(4,20)}$ = 1.647) nor is the slope of the regression line significantly different from zero (Table 10.9). Figure 10.5C has a regression line with a gradient less than unity (by a marginal amount, Table 10.10), which indicates very slight anti-apostatic selection. Because of zeros in the data, the results were totalled at each frequency and this may account for the difference in direction of the frequency-dependent selection in Figures 10.5B and 10.5C. The within-frequency variation of the data obtained at this prey density was very great. If the regression lines are compared with their respective regression lines from Experiment 9b, there are no significant differences between the slopes (β_T: $F_{(2,9)}$ = 1.503; Greenwood & Elton: $F_{(2,9)}$ = 0.080).

Figure 10.6 represents the results obtained at the density of 30 prey/m^2. There is a possible sigmoidal relationship indicated in Figure 10.6A. However, the scatter of the points within each frequency in Figure 10.6B precludes the negative slope of the regression line from being statistically significantly different from zero (Table 10.9), (analysis of variance between frequencies: $F_{(4,20)}$ = 2.131, N.S.). The slope of the regression line in Figure 10.6C is less than unity, indicating, as in Figure 10.6B, anti-apostatic selection (Table 10). The regression lines were compared with those obtained in Experiment 9a and

TABLE 10.11: Experiment 9c - Comparison of β_Ts obtained at each frequency: F values from analysis of variance.

	SOURCE		
FREQUENCY GR:G	AMONG DENSITIES F(3,20)	LINEAR REGRESSION F(1,2)	DEVIATIONS FROM REGRESSION F(2,20)
1:9	3,837*	0,818	4,085*
3:7	0,149	0,160	0,206
5:5	1,667	0,002	2,498
7:3	5,323**	24,907*	0,594
9:1	0,675	0,163	0,936

Asterisks indicate level of statistical significance: *p<0,05, **p<0,01.

were found not to be significantly different (β_T: F(2,11) = 1.174; Greenwood & Elton: $F_{(2,11)}$ = 2.464).

Figure 10.7 shows the results from the density of 2 prey/m^2. The scatter within frequencies was large and none of the three graphs give any indication of frequency-dependent selection: indeed, the regression line drawn in Figure 10.7C almost exactly matches the line of random predation. The regression analyses for Figures 10.7B and 10.7C are given in Tables 10.9 and 10.10 respectively.

Figure 10.8 represents the results from the prey density of 1/4m^2. As in the results obtained at the density of 2 prey/m^2, there was very large within-frequency variation, and frequency-dependent selection is not apparent. Tables 10.9 and 10.10 give the regression analyses for Figures 10.8B and 10.8C.

There are no significant differences between the regression lines in graphs B ($F_{(3,12)}$ = 1.931) or in graphs C ($F_{(3,12)}$ =1.169).

The β_Ts obtained at each density for a particular frequency have been compared using analysis of variance. Table 10.11 summarises the results from this analysis.

At the 1:9 frequency (when **GR** was rare) there was a significant difference in the β_Ts between the four densities. This was not a linear regression, however.

At the frequency of 7:3 there was a significant difference between densities, which is caused by linear regression. The equation of the regression line is y = 43.950 + 0.004x and the gradient is significantly different from zero ($t_{(18)}$ = 3.355, $p<0.01$).

At all the other frequencies there were no significant differences between densities and there was no significant regression.

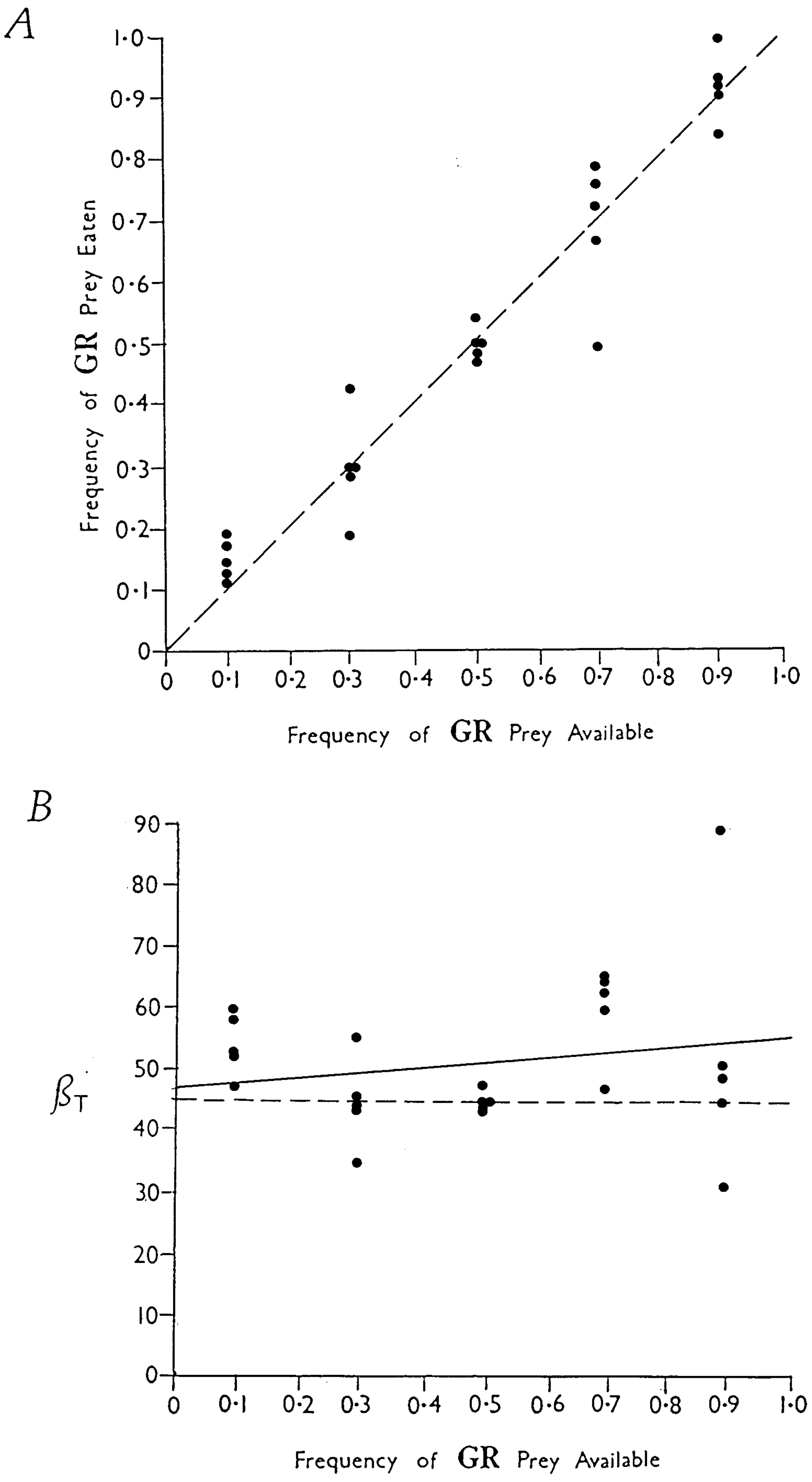
FIGURES 10.5, 10.6, 10.7 and 10.8: Experiment 9c. Frequency-dependent selection at the prey densities of $3850/m^2$ (Figure 10.5), $30/m^2$ (Figure 10.6), $2/m^2$ (Figure 10.7) and $1/4m^2$ (Figure 10.8).

Figures 10.5A, 10.6A, 10.7A and 10.8A: Frequency of **GR** prey eaten plotted against frequency of **GR** prey available. Broken lines represent expected relationship if prey were eaten in the proportions in which they were presented.

Figures 10.5B, 10.6B, 10.7B and 10.8B: β_T (selection against **GR**) plotted against frequency of **GR** prey available. Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Manly, 1973.)

Figures 10.5C, 10.6C, 10.7C and 10.8C: $Log(e_1/e_2)$ (Figures 10.6C and 10.7C) or $Log(\Sigma e_1/\Sigma e_2)$ (Figures 10.5C and 10.8C) (where e_1 and e_2 are the numbers of **GR** and **G** prey eaten) plotted against $Log(A_1/A_2)$ (where A_1 and A_2 are the numbers of **GR** and **G** prey available). Broken lines represent the expected relationship if there was no selection. The solid lines were fitted by linear regression. (Analysis following Greenwood and Elton, 1979.)

FIGURE 10.5: Experiment 9c. 3850 prey/m^2.



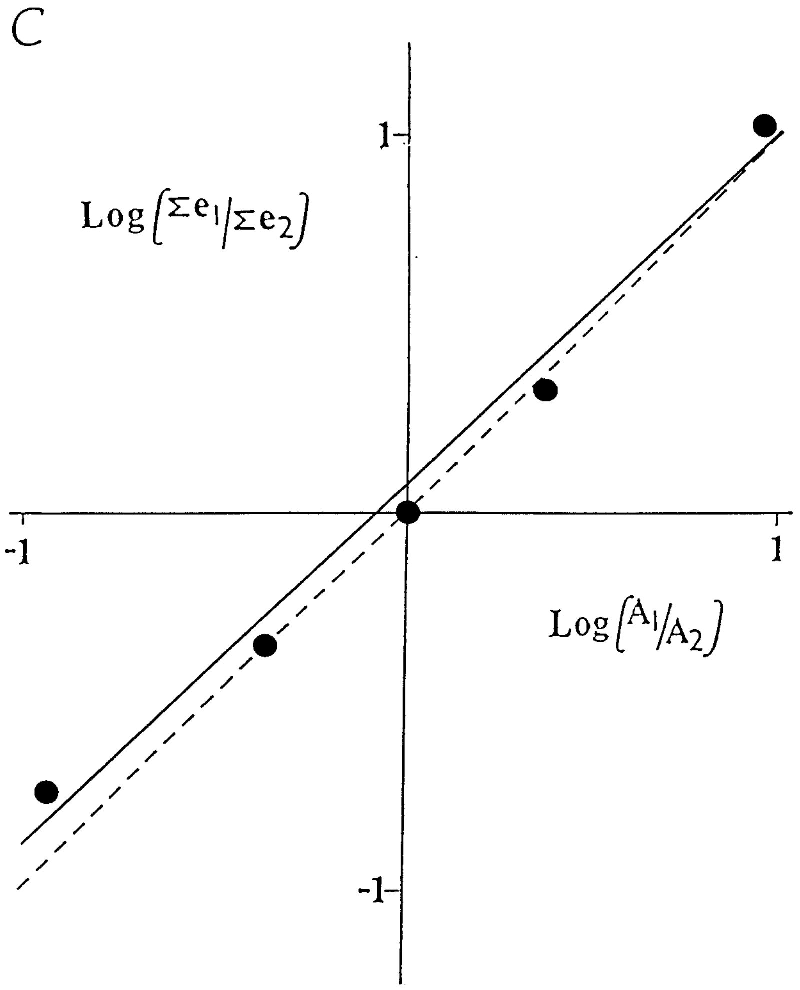
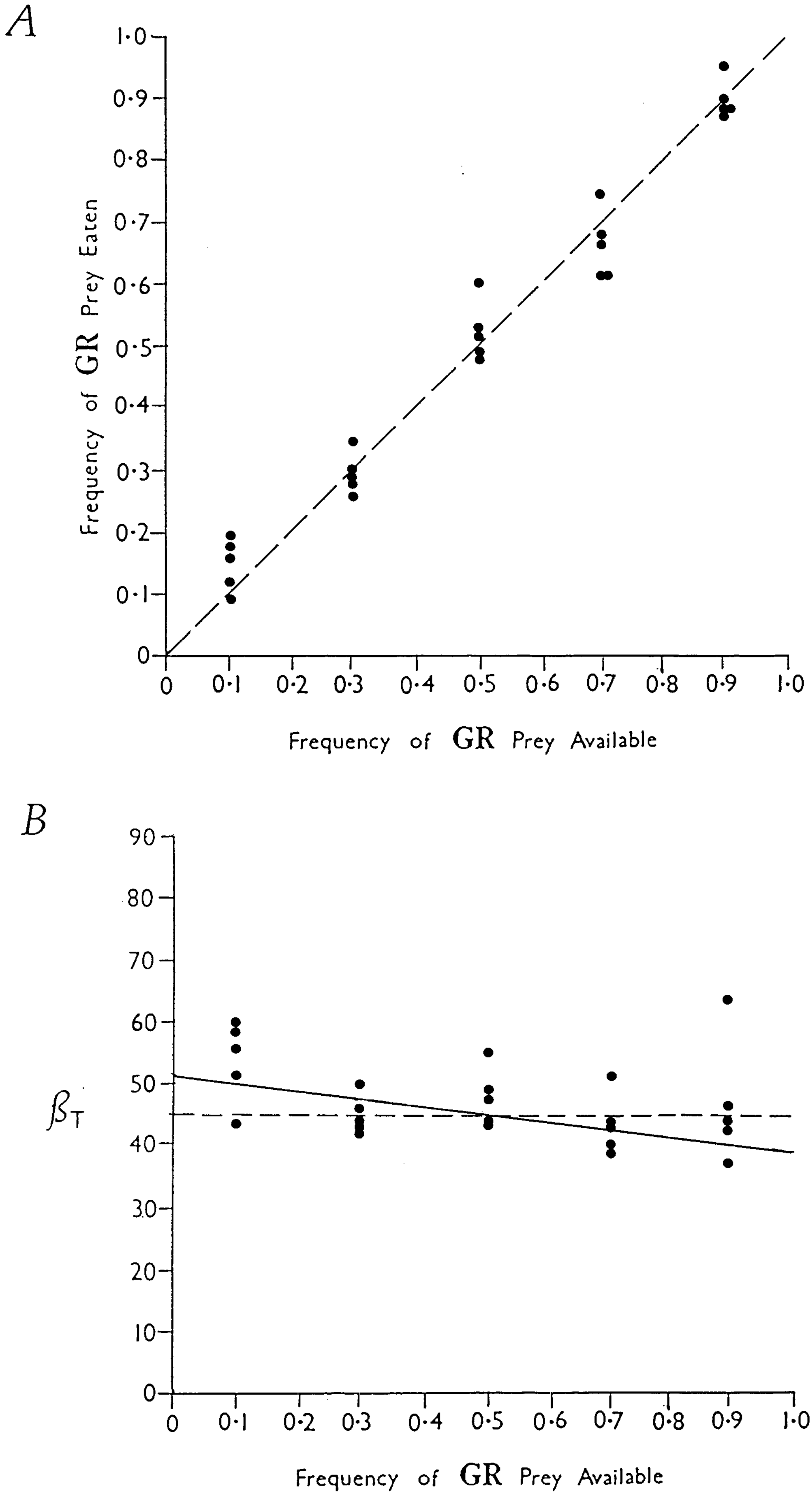

C
1
-1
-1
1
Log(Σe1/Σe2)
Log(A1/A2)

FIGURE 10.6: Experiment 9c. 30 prey/m^2.



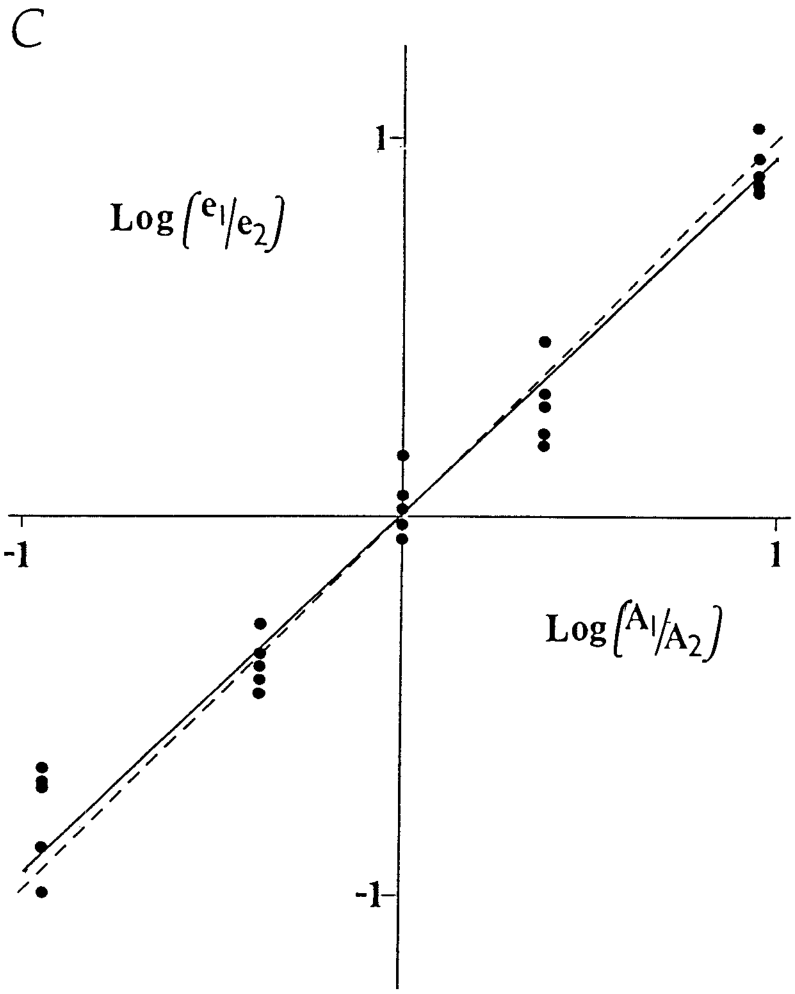
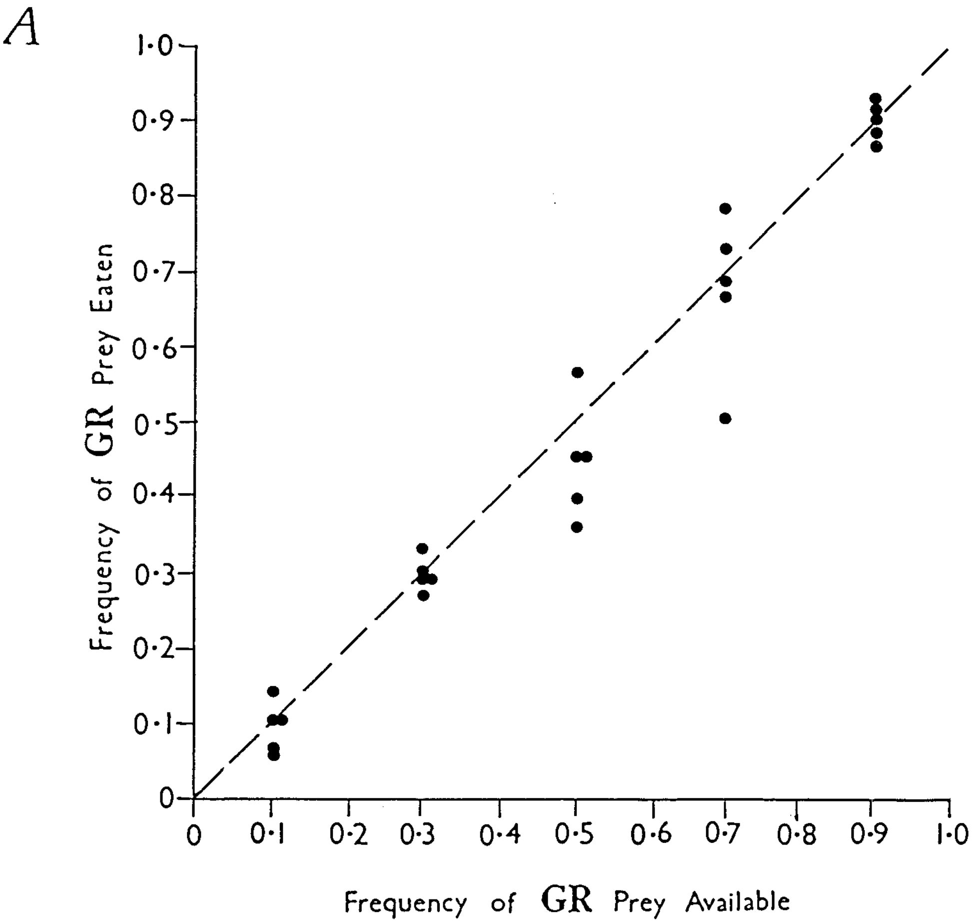
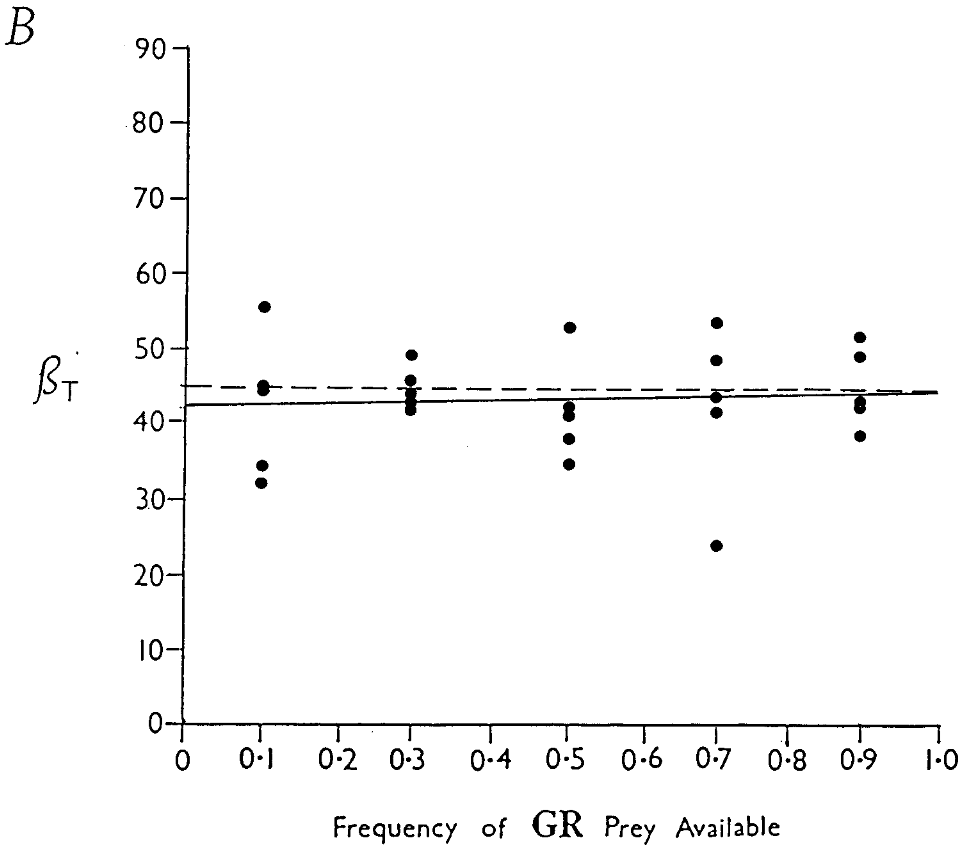

C
1
-1
Log (e_1/e_2)
-1
1
Log (A_1/A_2)

FIGURE 10.7: Experiment 9c. 2 prey/m^2.





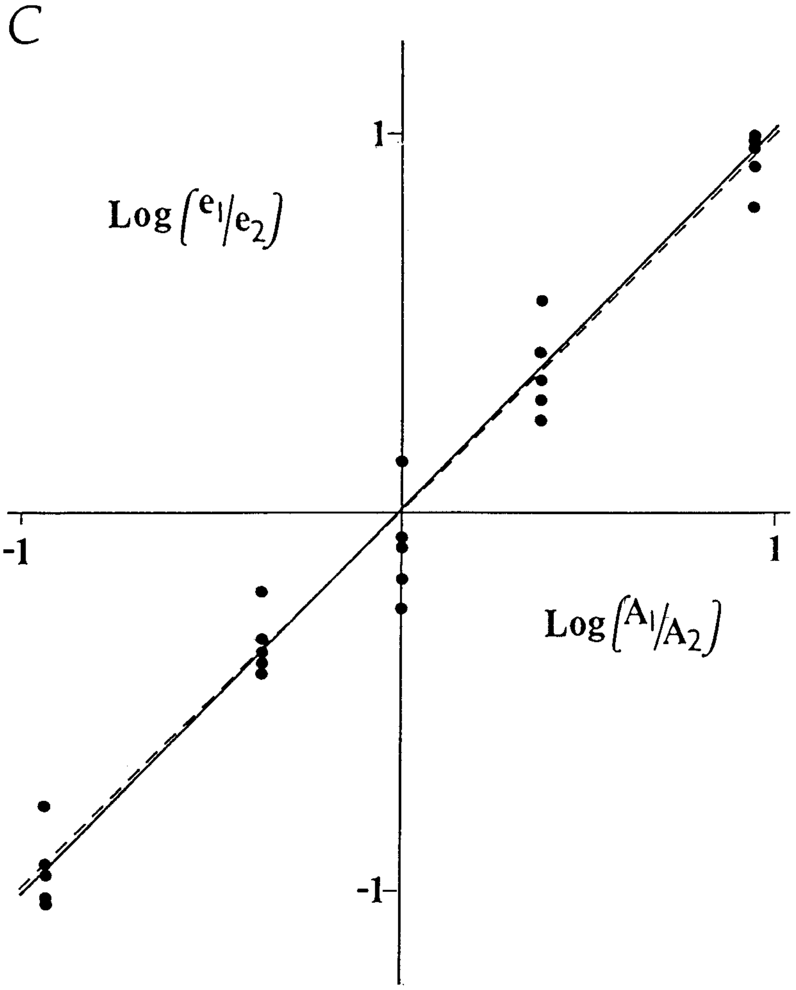
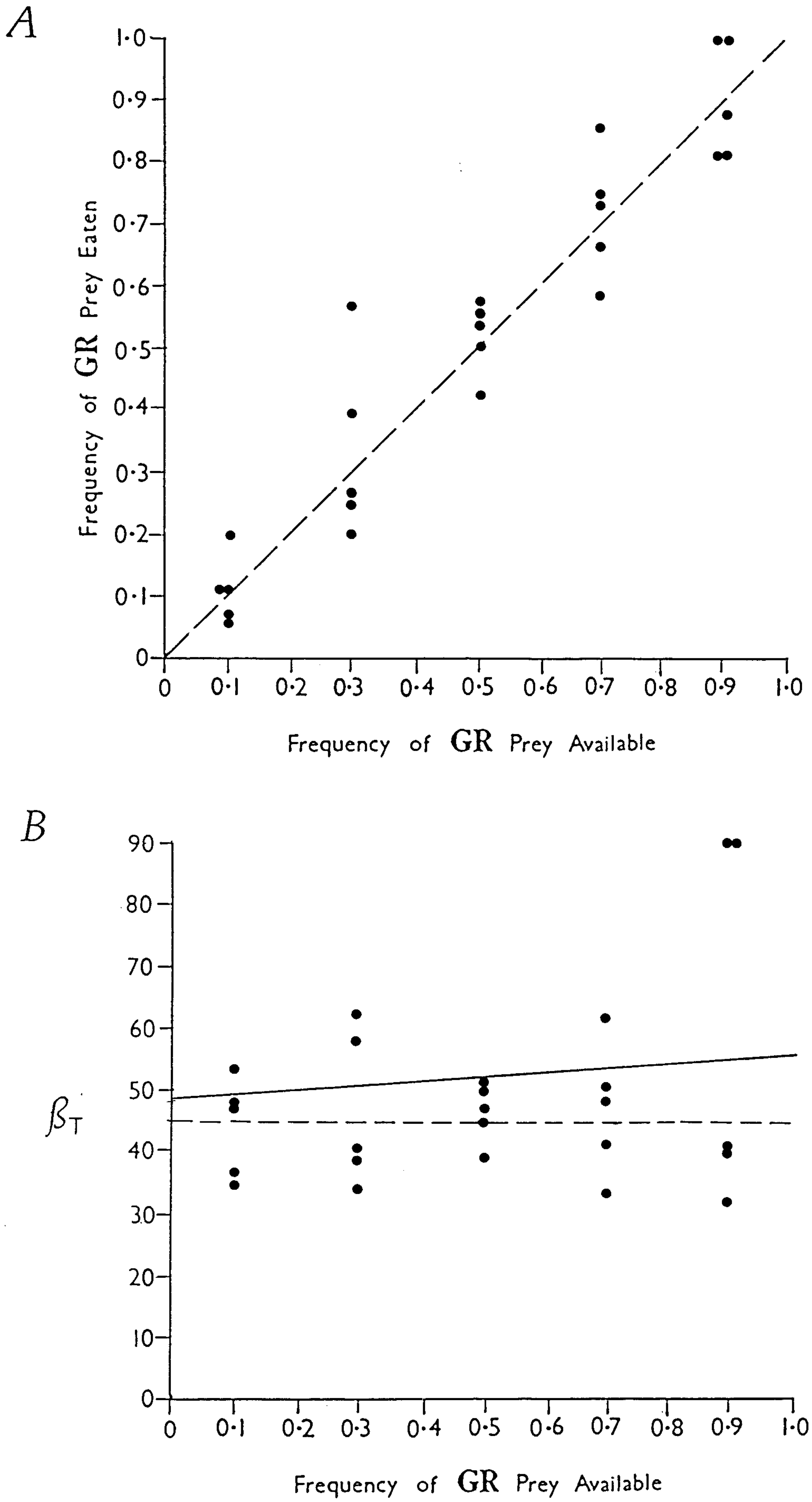
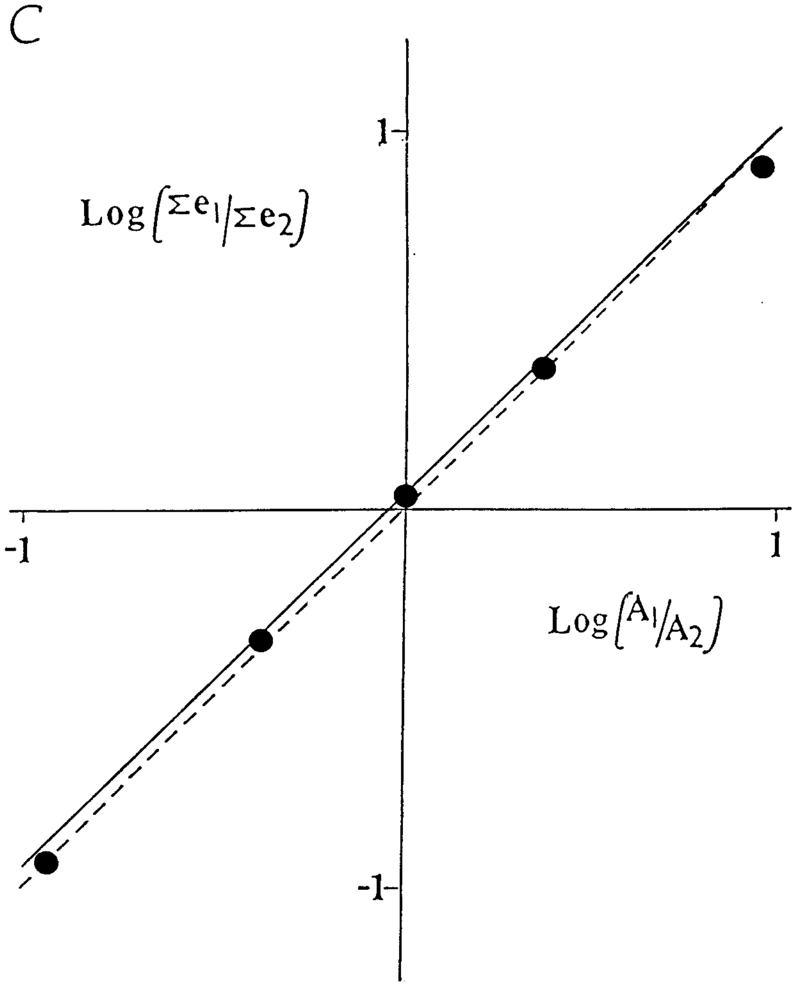

C
1
Log (e1/e2)
-1
1
Log (A1/A2)
-1

FIGURE 10.8: Experiment 9c. 1 prey/4m^2.




C
1
-1
-1
1
Log(Σe1/Σe2)
Log(A1/A2)

10.4 DISCUSSION

In Experiment 9a, where the prey were presented at the density of 30/m^2, anti-apostatic selection was demonstrated at both sites. The selection at Site 2 appeared to be stronger than the selection at Site 1; however, two more prey frequencies were presented at Site 2 and this factor alone may account for the higher levels of statistical significance obtained for both regression lines from Site 2. Support for this explanation comes from statistical analysis of the data from Experiment 9a, Site 2, leaving out data from the two 'extra' frequencies of 2:8 and 8:2. The two regression lines obtained from this analysis have less significant slopes than the two original slopes (compare with Tables 10.4 and 10.5: β_T: $t_{(23)} = 3.289$, $p<0.01$; Greenwood and Elton: $t_{(23)} = 2.228$, $p<0.05$).

Anti-apostatic selection was also detected at the density of 30 prey/m^2 in Experiment 9c, although the design of this experiment appeared to reduce the effects of any selection. The use of a number of different prey densities in a random order probably affected the feeding behaviour of the birds: it would have been as if a prey population constantly shifted between a clumped and a spaced out distribution. Regular predators, on each arrival at the site, may have 'expected' to find a prey population of the same density as that they had last experienced, confusion may have resulted in the birds being less selective when they found the new prey population. Another factor may have been that the majority of predation in Experiment 9c was by starlings, and observation indicated that they took prey that were at the edge of the prey population, unlike the birds in Experiment 9a.

At all three sites, preferences for the **GR** prey type were indicated. The probability is that this preference was due to the greater conspicuousness of the **GR** prey over the **G** prey. Previous experiments using these two prey types appear to confirm this assumption (Chapters 4 and 6). Any other explanation would have to account for the preference occurring in many different species of birds (and therefore in many different individuals) at many sites and at different times of the year. If this preference was due to relative conspicuousness, then the choice between prey types at the density of 30 prey/m^2 was not an equal one. The apparent relative frequencies of the two prey types as observed by a predator might have been affected by the difference in conspicuousness: the **GR** prey type might have appeared the most common to the birds because they saw more of them. Unless this frequency-independent selection was so strong that only the preferred prey type was eaten, then frequency-dependent selection might still occur but, using either of the methods of statistical analysis (Manly, 1974 or Greenwood and Elton, 1979), any regression lines obtained would lie parallel to the lines of frequency-dependent selection in the absence of frequency-independent selection.

At the density of 30 prey/m^2, most of the prey would have been within the direct detection distance (Tinbergen *et al.*, 1967) for a bird, such as a blackbird, starling or pigeon, feeding from the ground within or immediately around the experimental area. From a bush or tree that was fairly close to the experimental area (and there were many at each site), all birds would have had a clear view of the experimental area and of the prey. This meant that, provided a bird could detect both prey types equally, it had an equal choice as to which prey item it would take. In other words, the distances between prey items were such that a predator did not have to search between prey items.

Greenwood (1984) suggests that the explanation for anti-apostatic selection occurring at densities that are high but not at 'maximum' (contiguous prey) might be that animals may be confused by the presence of more than one prey item in their sensory field at any one time. He states that "it seems probable that an animal will be more efficient if it attends to prey that differ from all the other prey that are in its sensory field than if it tries to attend to individuals that are similar to many of the others that are present". This theory is also based on the observations that predators tend to feed on stragglers or 'odd' prey types in herds, flocks or swarms (Milinski, 1977a,b; Pielowski, 1959; Ohguchi, 1978, 1981; Landeau and Terborgh, 1986). This explanation would also apply to anti-apostatic selection at very high prey densities where the prey were contiguous ('maximum' density), with the extension that the commoner prey type becomes the background against which the rarer prey type is viewed by the predator, and this contrast makes it easier for the predator to take a single rare form than a single common form.

Experiment 9b presented predators with prey at 'maximum' density. The results indicated apostatic rather than anti-apostatic selection at Site 1 and very slight anti-apostatic selection at Site 2. At 'maximum' density in Experiment 9c, only very slight anti-apostatic selection was found using the method of Greenwood and Elton (1979). At this density, there was no evidence for any frequency-independent prey preferences.

The behaviour of many of the birds when confronted with the prey population at this density was interesting. Observation indicated that the birds, particularly the starlings that accounted for the majority of the predators in Experiment 9b, Site 2 and in Experiment 9c, initially treated the mass of prey very warily. They then attacked the outer edge of the prey mass, taking those prey items that were nearest to them, and then often moved away in an alarmed manner from the rest of the prey population to eat their 'captured' prey. If the birds always took the nearest prey the result would be random predation; if the birds frequently took the nearest prey the result would be a reduction in the significance of any frequency-dependent effects. Sometimes a bird would actually land on top of the prey mass, which would result in some prey being trodden on and broken and this made very accurate counting of prey eaten difficult. The behaviour of the birds at this prey density is therefore very different from the behaviour of the birds at the lower prey densities.

Allen (1972) was the first to detect anti-apostatic selection in artificial prey. He presented green and brown pastry prey in the ratios 1:9 and 9:1 in two metal sieves 1m apart to a pair of wild blackbirds. The prey populations were presented daily for 2 to 4 hours. Eaten prey were constantly replaced and the relative positions of the prey were frequently altered. The blackbirds tended to select the rarer colours.

Harvey, Jordan and Allen (1974) repeated this experiment with the two prey populations 2 km apart and found selection against the commoner prey type. They suggested that Allen's earlier result could have arisen from the birds establishing a preference for the commoner prey type in one sieve and then continuing to feed on this prey type if they transferred over to the other sieve. Since observation of the behaviour of the feeding birds in Allen's experiment was not continuous, it is unclear whether the birds did transfer from one sieve to the other.

Horsley *et al.* (1979) disagree with the explanation of Allen's result given by Harvey *et al.*, arguing that it would only hold if there was an increase in preference by the birds when they moved to the sieve where the preferred prey was rare or if the birds had systematically taken more prey from that sieve than from the other. They suggest that this is unlikely and that the differences between the results obtained from the two sets of experiments were due to differences between individual birds.

Horsley *et al.* (1979) used a 'maximum' prey density of approximately 11000/m^2 for three series of experiments. They repeated both the experiments of Allen (1972) and Harvey *et al.* (1974) and also presented prey populations serially. In a fourth series of experiments they presented prey populations at five different frequencies at a lower density of 800 prey/m^2. Series I confirmed the findings of Allen (1972). Series II found a greater difference within sites where the same prey type was rare than between sites where different prey types were rare. They suggested that individual preferences were so strong that they overshadowed any frequency-dependent effects. Series III was designed to overcome this problem. They presented populations of the two prey types at twelve sites: at six sites the prey were presented in the ratio 9:1 and at the other six in the ratio 1:9. After a few days they reversed the proportions of the two prey types. Thus any differences between sites could be overcome by comparing the selection after the change in proportions with that before it. Their results were very clear. At each site the birds ate disproportionately more rare prey. They also found significant heterogeneity between sites at which the same prey type was rare. They showed that the birds selected the rare form more strongly after they had experienced prey populations in which it was common. This might indicate that the birds did not treat the common prey type as purely 'background' to the rare prey type. Series IV varied the frequency of prey offered at different sites at the lower density of 800 prey/m^2. They plotted the proportion of one prey type eaten against the proportion of that prey type presented and obtained a sigmoidal line of best fit that indicated anti-apostatic selection. Using the analytical methods of Elton and Greenwood (1970), they obtained a value of b that was less than unity, again representing anti-apostatic selection. This final series was a high density experiment but one that did not use the maximum density and therefore the birds were not seeing a contiguous prey mass. Thus the explanation proffered by Greenwood (1984) relating this response to confusion of the sensory field, given earlier in this discussion, would be relevant to this experiment.

Allen and Anderson (1984) attempted to overcome some of the criticisms of the work of Allen (1972) in two series of experiments. In Series I they presented five prey populations containing different pairs of prey colours in the ratio 1:9 simultaneously. Therefore if a bird fed on one prey population and then transferred to another prey population it would not encounter the same prey type twice and any preferences it might have developed should not affect its prey choices. The prey density was 'maximum' (approximately 11800/m^2) and the populations were contained in foil dishes. Two sites, 200 m apart, were used simultaneously, with the pairs of colours in opposite ratios. The populations were presented in the morning and removed late afternoon and the numbers of each prey colour taken were recorded. New populations were put out each morning over a period of 35 days. After a few days break the experiment was repeated with the prey colours in the reverse ratios. Comparison therefore could be made both between sites and within sites. They calculated Manly's β for each population and each day. In the first experiment they found selection against the rare prey colours in four out of five populations at both sites. In the repeat experiment, where the ratios of the colours were reversed, they found selection against the rare prey colour in all prey populations. The degree of selection by the birds was also influenced by which pair of prey colours they encountered.

In their second series of experiments, Allen and Anderson repeated the experiment of Allen (1972) using three captive blackbirds so that careful behavioural observation could be made regarding the movements of the birds between prey populations. The two prey populations were presented for two hours each day for six days. Pooling the data from the three birds shows that they were selecting against the rare prey colours in both prey populations. Observations of the individual birds found that each bird tended to concentrate on one prey colour over the course of each experimental period irrespective of prey population. It was rare for the birds to switch over from one population to the other during a visit and there was also a tendency for the birds to revisit the dish that they had previously fed from. In ten out of eighteen instances, the birds took the rare prey colour during their first visit of the day. The observations do not support the hypothesis of Harvey *et al.* that birds start by feeding on the common form in one prey population and then continue to feed on this colour in the second prey population.

Allen and Anderson suggest that birds are conservative in their choice of prey colours and that if they consistently preyed on only one colour each day then the pooled result would be anti-apostatic selection. Observations during my experiments do not give similar results from the feeding behaviour of the birds. Although much of the feeding was done by birds such as sparrows and starlings that tend to feed in groups and are not individually recognisible, in the instances where results were obtained for individual birds, they did not usually feed exclusively on either prey type at any density (see Appendix at end of this chapter for data). However, the similarity between prey types in my experiments was considerably greater than in those of Allen and Anderson, and my results exclude the explanation for anti-apostatic selection they suggested. The more likely explanation would seem to be that given by Greenwood (1984). Clearly we need more observations of the birds' feeding behaviour in these sorts of experiments.

Two lower prey densities were also used in Experiment 9c: $2/m^2$ and $1/4m^2$. There was considerable heterogeneity between replicates at each prey frequency. No frequency-dependent selection at these two densities was apparent. At prey densities which are so low that the time between prey capture is relatively long, rejection of any prey found might not result in the predator foraging optimally. It is possible that the result from my experiment at the lowest prey density was due to this factor; although starlings, the main predators, do not appear to exhibit strong frequency-dependent feeding behaviour.

Nearly all predation in Experiment 9c was due to starlings, whereas sparrows and blackbirds contributed substantially to predation in Experiments 9a and 9b (Table 10.2). Observation indicated that starlings were preying randomly: taking whichever prey type was nearest. They fed in small flocks most of the time. When the lower densities of prey were presented, if one starling found a prey item the other starlings would join it and then move across the grass searching for other prey, eating those found as they went. Thus <u>all</u> prey within an area of grass were usually eaten and the result, of course, was random predation. Although sparrows also fed in groups, a bird would appear to choose a prey item from a vantage point in a bush or tree surrounding the experimental area and would then fly down to eat it. Other sparrows might fly down and share the prey and perhaps move to the immediately adjoining areas but they would not stay on the ground searching for very long. This behaviour was observed at the prey density of $2/m^2$ at two sites in training experiments (Chapter 6). Species differences have been observed before in experiments reported in other chapters and starlings do not appear to be particularly selective in their feeding behaviour. There is no real evidence from this experiment that the changes in prey densities affected the prey selection by the starlings relating to frequency-dependent selection; although there was density-dependent behaviour by the starlings with regard to their methods of predation, but this resulted in, what was in effect, random predation. However, differences between the four prey densities used in Experiment 9c were seen in comparisons of the β_Ts obtained at each of the five prey frequencies (Table 10.11). At the frequency of **1GR**:**9G**, there was a significant difference in the results from each density. There was no linear regression at the frequency of **1GR**:**9G** but at the prey frequency of 7**GR**:3**G**, there was a significant linear regression between the prey densities, and the slope of the line showed that, as the prey density increased, relatively more of the common (**GR**) prey were eaten. This increase in common prey being eaten with increasing prey density is in the opposite direction from that which might be predicted since this would result in stronger apostatic selection at the high prey densities at this frequency. No significant differences between densities were found at the other prey frequencies. Replicates of this experiment are needed, preferably with other species of birds, before any firm conclusions can be made.

Other workers have found apostatic selection at prey densities similar to the density of $2/m^2$ used in Experiment 9c. Following work by Allen and Clarke (1968), Allen (1976) presented populations of green and brown pastry prey in the proportions of either 1:9 or 9:1 and at the density of $2/m^2$ (one of the densities used in Experiment 9c) to wild passerine birds in fourteen experiments over a period of three years. In seven experiments, a 1:9 prey population was presented for one week followed by a 9:1 prey population, and in the other seven experiments the populations were presented in the reverse order. The resulting numbers of each prey type eaten in each experiment were analysed and the overall trend was one of apostatic selection although significant heterogeneity within experiments precluded the results being conclusive.

Manly, Miller and Cook (1972) used the higher prey density of $5/m^2$ in experiments with domestic quail *Coturnix c. japonica*. Seven frequencies of red and blue pastry prey were used and there was a tendency for the birds to eat disproportionately more of the commoner colour. Following this work, Cook and Miller (1977) also presented quail with populations of various frequencies of blue and red pastry prey. They used four prey densities: $1.25/m^2$, $2.5/m^2$, $5/m^2$ and $7.5/m^2$. The results suggest that there was apostatic selection at all prey densities but at the prey densities of $1.25/m^2$ and $7.5/m^2$ it was extremely weak.

More recent experiments have found apostatic selection at apparently high densities. Fullick and Greenwood (1979) presented White Leghorn chicks with populations of green and brown chick crumbs. The density used was $2083/m^2$ and the frequencies ranged from 0.025 to 0.9. Eighty birds were used, one for each trial. Five trials were done for each prey frequency. Predation was halted when one-tenth of the chick crumbs had been eaten. The results clearly showed apostatic selection. However, similar experiments by Willis *et al.* (1980) did not show frequency-dependent selection. As well as using a range of prey frequencies, they used three prey densities: $606/m^2$, $2425/m^2$ and

4850/m^2. Although these appear to be high densities, at least 96% of the floor area was uncovered, which was also true of the experiments of Fullick and Greenwood. At all densities, the results indicated only extremely slight frequency-dependent selection but there was evidence for density-dependent selection with this selection being strongest at the intermediate density. Other experiments using only the prey density of 2425/m^2, but with three different prey colours presented in pair-wise combinations, also indicated that selection was only slightly, if at all, frequency-dependent.

The ground colour of my prey was designed to be a good match to the overall impression of the grass used as a background. The experiments of other workers discussed above did not use prey that were designed to match their backgrounds. Cooper (1984b) found that frequency-dependent selection was stronger when his 'pastry' prey matched the background than when they did not. He used a hessian cloth scattered with stones as the background for the prey. The colours of the stones could be varied to provide different backgrounds. Three backgrounds were used: a 'matching' background comprised of orange and grey stones, and two types of 'control' backgrounds composed of either lilac and yellow stones or all green stones. Seventeen frequencies of prey were presented to wild passerine birds on each of the three backgrounds in a random order (resulting in a total of 51 experiments). The prey density was 9/m^2. Predation was stopped when approximately half the prey had been eaten and there were four successive trials at each prey frequency on each background. On each background the birds appeared to feed apostatically. Manly's β (arcsin transformed) was plotted against frequency of grey prey available and significantly positive regression slopes were obtained. Apostatic selection was stronger on the 'matching' background than on either of the other two backgrounds.

Prey density has been shown to affect the direction of frequency-dependent prey selection by birds. Variations between results obtained in separate experiments have often been attributed to differences in the behaviour of species or individuals. At the higher densities, where most of the prey are within the detection distance of the predator, the selection is anti-apostatic in some experiments (Experiment 9a; Allen, 1972; Horsley *et al.*, 1979; Allen and Anderson, 1984), apostatic in others (Experiment 9b, Site 1; Fullick and Greenwood, 1979) or there is no frequency-dependent selection (Experiment 9b, Site 2; Experiment 9c; Willis *et al.*, 1980). At the lower densities, if frequency-dependent selection is found, selection is apostatic (Manly *et al.*, 1972; Allen, 1976; Cook and Miller, 1977; Cooper, 1984b). At very low prey densities there is no evidence of frequency-dependent selection (Experiment 9c), although little work has been done. Further experiments at very low prey densities is needed to confirm these results.

10.5 SUMMARY

1. The density of prey has been shown to have an affect upon the direction of any frequency-dependent selection. The experiments reported in this chapter used a range of prey densities and a range of prey frequencies at a number of sites in order to examine frequency-dependent selection on plain and striped prey.
2. The prey densities were 3850/m^2 ('maximum'), 30/m^2, 2/m^2 and 1/4m^2. It was felt that this provided a good range of prey densities: a continuous prey mass through to widely spaced prey where a predator could see only one prey item at a time.
3. A range of prey frequencies was used to allow statistical analysis, using both the methods of Manly (1974) and Elton and Greenwood (1970).
4. The prey were those already used in previous experiments: plain green (**G**) and green with a red stripe (**GR**).
5. In all experiments wild birds were presented with prey populations made up of the two prey types in the appropriate prey frequency and at the appropriate prey density. The order in which the prey frequencies were presented was chosen at random. All populations were presented on grass lawns.
6. There were three experimental series: in Experiment 9a the prey density was 30/m^2 with five prey frequencies (1:9, 3:7, 5:5, 7:3, 9:1) at one site and seven frequencies (1:9, 2:8, 3:7, 5:5, 7:3, 8:2, 9:1) at the other site; in Experiment 9b the density was 3850/m^2 with five prey frequencies, as in Experiment 9a Site 1, at both sites; in

Experiment 9c all four prey densities and five prey frequencies were varied in a random order.

7. Anti-apostatic selection was demonstrated at the prey density of $30/m^2$ (Experiments 9a and 9c).

8. At the 'maximum' density (Experiments 9b and 9c), apostatic selection was detected at Site 1 Experiment 9b and very slight anti-apostatic selection at Site 2 Experiment 9b and Experiment 9c.

9. No frequency-dependent selection was apparent at the two lower prey densities of $2/m^2$ and $1/4m^2$ in Experiment 9c.

10. Possible reasons for the differences in direction and intensity of frequency-dependent selection are discussed.

APPENDIX TO CHAPTER 10

1. Original data for Experiment 9a

SITE 1

	FREQUENCY		NUMBERS TAKEN					
DATE	GR:G	TRIAL	GR	G	T	β	β_T	Log(GR/G)
27.4.84	1:9	1	3	27	30	0.500	45.00	-0.9542
		2	3	17	20	0.647	53.55	-0.7533
		3	5	29	34	0.699	56.75	-0.7634
		4	3	26	29	0.513	45.77	-0.9379
		5	5	21	26	0.784	62.33	-0.6233
19.4.84	3:7	1	17	24	41	0.773	61.57	-0.1498
		2	10	15	25	0.647	53.57	-0.1761
		3	14	16	30	0.758	60.55	-0.0580
		4	13	18	31	0.696	56.53	-0.1413
		5	8	11	19	0.659	54.29	-0.1383
17.4.84	5:5	1	20	6	26	0.831	65.74	0.5229
		2	11	12	23	0.472	43.40	-0.0378
		3	14	10	24	0.608	51.23	0.1461
		4	17	13	30	0.596	50.51	0.1165
		5	17	16	33	0.523	46.33	0.0263
		6	19	9	28	0.738	59.20	
		7	15	9	24	0.660	54.35	
		8	13	12	25	0.527	46.52	
		9	12	14	26	0.448	42.03	
		10	12	14	26	0.448	42.03	
26.4.84	7:3	1	16	6	22	0.542	47.40	0.4260
		2	18	10	28	0.408	39.72	0.2553
		3	11	8	19	0.341	35.71	0.1383
		4	20	13	33	0.335	35.39	0.1871
		5	16	6	22	0.542	47.40	0.4260
22.4.84	9:1	1	19	2	21	0.517	45.96	0.9777
		2	17	3	20	0.353	36.45	0.7533
		3	22	1	23	0.742	59.45	1.3424
		4	17	4	21	0.256	30.40	0.6284
		5	27	4	31	0.387	38.46	0.8293

SITE 2

DATE	FREQUENCY GR:G	TRIAL	NUMBERS TAKEN GR	G	T	β	β	Log(GR/G)
7.6.84	1:9	1	4	25	29	0.639	53.05	-0.7959
		2	5	28	33	0.710	57.43	-0.7482
		3	3	21	24	0.585	49.87	-0.8451
		4	3	28	31	0.487	44.24	-0.9700
		5	3	19	22	0.615	51.66	-0.8016
6.6.84	2:8	1	6	20	26	0.563	48.59	-0.5229
		2	6	18	24	0.596	50.53	-0.4771
		3	5	23	28	0.452	42.27	-0.6628
		4	4	19	23	0.446	41.89	-0.6767
		5	6	24	30	0.500	45.00	-0.6021
14.6.84	3:7	1	8	22	30	0.442	41.67	-0.4393
		2	5	15	20	0.424	40.64	-0.4771
		3	10	18	28	0.592	50.28	-0.2553
		4	8	16	24	0.551	47.91	-0.3010
		5	9	20	29	0.517	46.00	-0.3468
4.6.84	5:5	1	9	12	21	0.411	39.88	-0.1249
		2	11	9	20	0.562	48.53	0.0872
		3	14	20	34	0.364	37.11	-0.1549
		4	16	16	32	0.500	45.00	0
		5	10	14	24	0.392	38.77	-0.1461
12.6.84	7:3	1	13	7	20	0.429	40.93	0.2689
		2	20	9	29	0.483	44.01	0.3468
		3	19	10	29	0.426	40.75	0.2788
		4	16	5	21	0.596	50.52	0.5052
		5	17	7	24	0.513	45.75	0.3854
13.6.84	8:2	1	23	7	30	0.427	40.80	0.5166
		2	29	10	39	0.341	35.72	0.4624
		3	16	4	20	0.500	45.00	0.6021
		4	23	7	30	0.427	40.80	0.5166
		5	22	7	29	0.412	39.92	0.4973
8.6.84	9:1	1	18	3	21	0.369	37.41	0.7782
		2	19	4	23	0.283	32.14	0.6767
		3	28	4	32	0.400	39.20	0.8451
		4	32	3	35	0.564	48.72	1.0280
		5	25	3	28	0.473	43.45	0.9208

2. Original data for Experiment 9b

SITE 1

DATE	FREQUENCY	TRIAL	NUMBERS TAKEN			β	β_T	Log(ΣGR/ΣG)
	GR:G		GR	G	T			
10.7.84	1:9	1	4	31	35	0.563	48.61	
		2	4	38	42	0.475	43.54	
		3	0	28	28	0.000	00.00	
		4	2	33	35	0.300	33.23	
		5	0	20	20	0.000	00.00	-1.1761
13.7.84	3:7	1	8	21	29	0.459	42.64	
		2	5	16	21	0.404	39.48	
		3	8	17	25	0.531	46.79	
		4	7	20	27	0.432	41.11	
		5	6	22	28	0.353	36.47	-0.4508
2.7.84	5:5	1	15	13	28	0.550	47.85	
		2	11	10	21	0.530	46.71	
		3	21	15	36	0.635	52.81	
		4	14	19	33	0.385	38.36	
		5	12	16	28	0.401	39.31	0
4.7.84	7:3	1	19	9	28	0.465	42.99	
		2	11	4	15	0.547	47.71	
		3	25	9	34	0.566	48.80	
		4	17	9	26	0.428	40.86	
		5	13	2	15	0.759	60.58	0.4109
15.7.84	9:1	1	31	2	33	0.678	55.42	
		2	43	4	47	0.592	50.28	
		3	20	3	23	0.400	39.25	
		4	24	4	28	0.349	36.18	
		5	22	4	26	0.323	34.61	0.9157

SITE 2

DATE	FREQUENCY	TRIAL	NUMBERS TAKEN			β	β_T	Log(GR/G)
	GR:G		GR	G	T			
2.8.84	1:9	1	3	19	22	0.615	51.66	-0.8016
		2	5	30	35	0.688	56.07	-0.7782
		3	2	21	23	0.452	42.22	-1.0212
		4	2	23	25	0.422	40.52	-1.0607
		5	3	23	26	0.555	48.18	-0.8846
27.7.84	3:7	1	10	11	21	0.728	58.54	-0.0414
		2	10	13	23	0.687	55.95	-0.1139
		3	8	15	23	0.571	49.08	-0.2730
		4	12	29	41	0.484	44.07	-0.3832
		5	11	31	42	0.414	40.02	-0.4500
25.7.84	5:5	1	17	21	38	0.410	39.81	-0.0918
		2	12	19	31	0.337	35.51	-0.1996
		3	9	12	21	0.411	39.88	-0.1249
		4	11	11	22	0.500	45.00	0
		5	12	11	23	0.528	46.60	0.0378
1.8.84	7:3	1	18	8	26	0.488	44.30	0.3522
		2	14	6	20	0.500	45.00	0.3680
		3	11	8	19	0.341	35.71	0.1383
		4	18	7	25	0.532	46.83	0.4102
		5	34	15	49	0.481	43.89	0.3554
26.7.84	9:1	1	29	3	32	0.526	46.51	0.9853
		2	30	2	32	0.667	54.74	1.1761
		3	28	3	31	0.513	45.76	0.9700
		4	44	4	48	0.606	51.09	1.0414
		5	31	3	34	0.552	47.98	1.0142

3. Original data for Experiment 9c

i) 3850/m^2

DATE	FREQUENCY GR:G	TRIAL	NUMBERS TAKEN GR	G	T	β	β_T	Log(ΣGR/ΣG)
15.5.84	1:9	1	3	19	22	0.615	51.66	
am		2	4	26	30	0.626	52.29	
		3	4	19	23	0.717	57.86	
		4	4	17	21	0.744	47.16	
		5	4	33	37	0.538	53.52	-0.7782
9.5.84	3:7	1	13	31	44	0.489	44.36	
am		2	10	23	33	0.506	45.32	
		3	9	12	21	0.673	55.13	
		4	4	17	21	0.326	34.84	
		5	7	17	24	0.487	44.25	-0.3665
14.5.84	5:5	1	15	13	28	0.550	47.85	
am		2	22	23	45	0.480	43.62	
		3	15	16	31	0.476	43.64	
		4	11	11	22	0.500	45.00	
		5	11	11	22	0.500	45.00	0
24.5.84	7:3	1	22	11	33	0.770	59.36	
pm		2	11	3	14	0.825	65.25	
		3	10	10	20	0.538	47.17	
		4	19	6	25	0.819	64.78	
		5	16	6	22	0.782	62.18	0.3358
10.5.84	9:1	1	26	0	26	1.000	90.00	
am		2	27	3	30	0.500	45.00	
		3	26	5	31	0.268	31.19	
		4	33	3	36	0.577	49.41	
		5	26	2	28	0.618	51.84	1.0259

ii) 30/m^2

DATE	FREQUENCY GR:G	TRIAL	NUMBERS TAKEN GR	G	T	β	β_T	Log(GR/G)
23.5.84	1:9	1	2	20	22	0.467	43.11	-1.0000
am		2	4	19	23	0.717	57.86	-0.6767
		3	5	26	31	0.732	58.81	-0.7160
		4	5	38	43	0.596	50.51	-0.8808
		5	6	31	37	0.677	55.39	-0.7132
2.5.84	3:7	1	9	17	26	0.572	49.14	-0.2762
am		2	10	23	33	0.506	45.32	-0.3617
		3	6	15	21	0.479	43.77	-0.3980
		4	6	17	23	0.439	41.48	-0.4523
		5	11	29	40	0.446	41.91	-0.4210
14.5.84	5:5	1	20	21	41	0.477	43.69	-0.0212
pm		2	17	16	33	0.523	46.33	0.0263
		3	13	14	27	0.475	43.55	-0.0322
		4	16	14	30	0.548	47.76	0.0580
		5	20	13	33	0.659	54.28	0.1871
21.5.84	7:3	1	27	9	36	0.598	50.63	0.4771
am		2	16	10	26	0.372	37.56	0.2041
		3	17	8	25	0.469	43.21	0.3274
		4	13	8	21	0.387	38.44	0.2109
		5	14	7	21	0.452	42.22	0.3010
4.5.84	9:1	1	25	3	28	0.473	43.44	0.9208
am		2	27	1	28	0.792	62.85	1.4314
		3	23	3	26	0.445	41.82	0.8846
		4	35	5	40	0.368	37.36	0.8451
		5	37	4	41	0.513	45.73	0.9661

iii) $2/m^2$

	FREQUENCY		NUMBERS TAKEN					
DATE	GR:G	TRIAL	GR	G	T	β	β_T	Log(GR/G)
21.5.84	1:9	1	4	37	41	0.487	44.27	-0.9661
pm		2	2	18	20	0.500	45.00	-0.9542
		3	5	31	36	0.677	55.39	-0.7924
		4	2	35	37	0.280	31.92	-1.2430
		5	2	32	34	0.311	33.90	-1.2041
16.5.84	3:7	1	11	27	38	0.478	43.76	-0.3900
pm		2	15	31	46	0.572	49.15	-0.3153
		3	7	17	24	0.487	44.25	-0.3854
		4	9	24	33	0.450	42.13	-0.4260
		5	7	16	23	0.507	45.38	-0.3590
25.5.84	5:5	1	8	12	20	0.378	37.93	-0.1761
am		2	9	16	25	0.319	34.38	-0.2499
		3	11	13	24	0.446	41.88	-0.0726
		4	24	18	42	0.637	52.96	0.1249
		5	16	19	35	0.432	41.07	-0.0746
23.5.84	7:3	1	24	12	36	0.435	41.29	0.3010
pm		2	18	17	35	0.162	23.75	0.0248
		3	22	10	32	0.478	43.73	0.3424
		4	19	5	24	0.649	53.68	0.5798
		5	27	10	37	0.559	48.41	0.4314
11.5.84	9:1	1	27	4	31	0.387	38.46	0.8293
pm		2	34	4	38	0.475	43.56	0.9294
		3	25	2	27	0.605	51.08	1.0969
		4	32	3	35	0.564	48.70	1.0280
		5	33	4	37	0.462	42.84	0.9165

iv) $1/4m^2$

	FREQUENCY		NUMBERS TAKEN					
DATE	GR:G	TRIAL	GR	G	T	β	β_T	Log(ΣGR/ΣG)
18.5.84	1:9	1	1	8	9	0.536	47.05	
am		2	2	16	18	0.550	47.88	
		3	1	15	16	0.333	35.26	
		4	3	12	15	0.652	53.82	
		5	1	14	15	0.357	36.68	-0.9542
17.5.84	3:7	1	4	3	7	0.792	62.88	
am		2	8	12	20	0.722	58.16	
		3	7	19	26	0.390	38.65	
		4	3	9	12	0.420	40.40	
		5	3	12	15	0.324	34.67	-0.3424
24.5.84	5:5	1	7	5	12	0.608	51.23	
am		2	9	7	16	0.593	50.37	
		3	7	7	14	0.500	45.00	
		4	6	8	14	0.401	39.31	
		5	7	6	13	0.552	47.97	0.0378
3.5.84	7:3	1	12	4	16	0.590	50.21	
am/pm		2	10	5	15	0.444	41.76	
		3	11	4	15	0.558	48.33	
		4	10	7	17	0.301	33.25	
		5	12	2	14	0.771	61.43	0.3979
17.5.84	9:1	1	11	0	11	1.000	90.00	
pm		2	9	2	11	0.270	31.28	
		3	9	0	9	1.000	90.00	
		4	14	3	17	0.380	39.20	
		5	7	1	8	0.425	40.71	0.9208

4. RESULTS FROM INDIVIDUAL SPECIES/BIRDS

EXPERIMENT 9a: SITE 1

5GR:5G

MALE BLACKBIRD (al)
Prey Taken
GR G G GR GR GR GR
GR G G GR GR GR
GR GR GR GR GR G G G GR
GR G GR
G G G GR GR
GR G GR GR G GR
GR GR G GR G GR G
GR G GR G GR ? G GR GR ? G G GR GR GR G GR ?

INDIVIDUAL SPECIES

	GR	G	T
Chaffinch	0	2	2
Sparrow	20	5	25
Male BB(al)	70	52	122

1GR:9G
Male BB(al) 3GR 25G

7GR:3G
Sparrows 18GR 10G

3GR:7G
–

9GR:1G
Male BB(al) 19GR 2G

EXPERIMENT 9a: SITE 2

1GR:9G
Sparrows 18GR 121G

3GR:7G
Sparrows 17GR 36G

7GR:3G
Sparrows 66GR 28G

9GR:1G
Sparrows 122GR 17G

2GR:8G
Sparrows 29GR 104G

5GR:5G
Sparrows 60GR 71G

8GR:2G
Sparrows 68GR 21G

EXPERIMENT 9b: SITE 1

1GR:9G
Male BB 0GR 48G

5GR:5G
Sparrows 62GR 63G

9GR:1G
Sparrows 75GR 9G

3GR:7G
Sparrows 11GR 38G

7GR:3G
Male BB 44GR 18G
Sparrows 13GR 4G

EXPERIMENT 9b: SITE 2

1GR:9G
Sparrows 3GR 9G

5GR:5G
Starlings 12GR 19G

9GR:1G
–

3GR:7G
–

7GR:3G
Sparrows 14GR 6G

EXPERIMENT 9c: 3850/m^2

1GR:9G
Starlings 19GR 114G

5GR:5G
Starlings 63GR 63G

9GR:1G
Starlings 138GR 13G

3GR:7G
Starlings 43GR 100G

7GR:3G
Starlings 51GR 27G

EXPERIMENT 9c: 30/m^2

1GR:9G
Starlings 17GR 92G
Female BB(y) 0GR 4G

5GR:5G
Starlings 70GR 64G

9GR:1G
Starlings 147GR 16G

3GR:7G
Starlings 42GR 101G

7GR:3G
Starlings 87GR 42G

EXPERIMENT 9c: 2/m^2

1GR:9G
Starlings 11GR 86G

5GR:5G
Starlings 8GR 12G
Woodpigeons 24GR 18G

9GR:1G
Starlings 12GR 15G

3GR:7G
Starlings 49GR 115G

7GR:3G
Woodpigeons 19GR 5G

EXPERIMENT 9c: 1/4m^2

1GR:9G
Starlings 4GR 38G

5GR:5G
Starlings 36GR 33G

9GR:1G
Starlings 39GR 6G

3GR:7G
Starlings 25GR 55G

7GR:3G
Starlings 33GR 11G

CHAPTER 11 GENERAL DISCUSSION

11.1 EXPERIMENTAL DESIGN

The flat design of the pastry prey used in the majority of experiments reported in this thesis proved to be successful because colour patterns could be added easily, and the problems encountered in trying to apply colour patterns to cylindrical prey were avoided (Turner, 1961; Rake, 1978). The prey were not designed to represent any natural prey species but were presumably not out of the range of natural prey in size, and they could fairly easily be handled by all bird species. Green is a ground colour found in many edible prey species. Patterns that are found only on the dorsal surface of an animal are also common (see also Chapter 1). The shape of the prey was similar to that found in nature in insects such as some beetles or in seeds such as those of the sunflower. Therefore, at least in size, shape, colour and pattern, the pastry prey were not 'unnatural'. The snail shells filled with pastry (Chapter 9) were clearly much closer to natural prey in appearance. Their use involved more variation among individuals of the same morph and it is possible that some birds had past experience with *Cepaea*. Both these variables occur in natural predator-prey systems. In spite of this, the birds responded in much the same way to the snail shells as they did to the pastry prey. This provides additional justification for the use of pastry prey in experiments on visual selection by predators.

Chapter 3 exposed some of the problems of predation experiments using artificial backgrounds. Natural habitats are complex and three-dimensional; the artificial backgrounds were relatively simple and two-dimensional. The results did indicate that on the striped background the striped prey were at a slight advantage over plain prey; even small differences in the conspicuousness of different prey types might result in small differences in their risks of predation. Other researchers have used flat backgrounds and have experienced the same problems (Sellers, 1980; Cooper, 1984a). The use of grass as a natural three-dimensional 'stripy' background proved successful in experiments reported in subsequent chapters. Artificial backgrounds that are three-dimensional are another alternative. For example, Cooper (1984a,b) invented the idea of scattering coloured stones onto hessian. Backgrounds of this kind could have stones of different densities, colours and proportions to make backgrounds that could be adapted for many predation experiments; although there remains the problem of whether prey, using this technique, are cryptic or masquerading or Batesian mimics (Cooper, 1984a,b).

The experiments reported in Chapters 3, 4 and 5 were simple choice tests, designed to show the relative fitnesses of the various prey types in the different experimental conditions imposed in each experiment. In all cases, equal numbers of each prey type were presented to the bird predators. Results from the experiments in Chapters 3 and 4 showed that the prey type that most closely matched the background was the 'fittest' in evolutionary terms. These experiments concentrated on the effects of colour patterns on the crypsis of the prey and showed that stripy prey were at an advantage on stripy backgrounds if the stripes of the prey were similar to the stripes of the background with regard to colour. Therefore, the use of choice tests was successful for testing relative fitnesses of prey and for discovering if predators could distinguish between prey types on the basis of colour patterns alone.

'Training' experiments were used in Chapters 6, 7 and 9 to test whether birds preferred the familiar of prey types that differed only in their colour patterns, and to test whether chicks preferred the prey type most similar to a familiar one in Chapter 8. It has been proposed that behaviour of this kind would lead to apostatic selection. Greenwood and Elton (1979) have suggested that training experiments are "relevant to situations in which the prey frequencies are spatially or temporally heterogeneous, in that the predator may not respond immediately to changes in prey frequencies as it moves from place to place or as seasonal changes occur". They suggest that the result may be that the predator's behaviour need not be frequency-dependent for there to be frequency-dependent selection on the prey population. They do not believe that such training experiments demonstrate frequency-dependent selection that is independent of the temporal heterogeneity of the prey frequencies (see also Greenwood, 1985). Under the conditions of spatial or temporal heterogeneity between prey populations a predator may feed on the prey type that is the most familiar, regardless of the actual prey frequencies in the population, but this would not result in frequency-dependent selection since the familiar prey type might be at any frequency in the population. Frequency-dependent selection would only occur if the familiar prey type was the commonest or the rarest prey type. If predators can be shown to form preferences for familiar prey types, perhaps because they are the most common and have been encountered most often, then rare types would be at an advantage and selection could be frequency-dependent. Therefore, it can be argued that training experiments do lend further evidence for predator behaviour that is frequency-dependent.

In order to investigate the effects of density on frequency-dependent selection, a range of prey frequencies was presented to the birds (Chapter 10). Experiment 9c, in which both prey frequency and density were changed in a random order, gave no conclusive results and this was attributed to a combination of the design of the experiment and the bird species that acted as the predators in the majority of trials. (The effects of bird species on the outcome of experiments will be discussed in a later section.) The design of Experiment 9c meant that regular bird visitors to the area encountered prey populations that changed from clumped distributions to distributions in which the prey were spaced out. These changes were random. If the birds had treated each new prey population independently then the results might have been more similar to those obtained in Experiments 9a and 9b where prey density was constant. However, it is possible, if not probable, that the behaviour of the birds was affected by previous experience. Thus, for example, if they returned to the experimental site and the last experimental prey population that they had fed on had been clumped then they might immediately search the relatively small area in which that previous prey population had been (as found by Croze, 1970). If the new population was at one of the low densities, the birds might search more actively in one area before moving out across the site. Alternatively, after feeding on a low density, birds searching the site and discovering a high density population might be less selective in their choice of prey. Therefore, this experimental design could result in random predation. In retrospect, an improvement to this experimental design would be to separate the different prey populations using longer periods of time, to ensure that each prey population was treated separately by the birds. The alternative would be to present the complete range of prey frequencies before changing the prey density so that only one variable is changed at a time.

11.2 DIFFERENCES BETWEEN BIRD SPECIES

As already discussed in previous chapters, the species of bird that acted as predator in the experiments was found to affect the outcome. For example, in Experiment 5a (training experiments at six sites) woodpigeons showed less response to training than did blackbirds, robins and sparrows. Similarly, the predation in the 1982 replicates of Experiment 3 was almost exclusively by feral pigeons and showed less selection than the 1983 replicates, in which predation was predominantly by blackbirds. Species differences in factors such as visual acuity and search methods are relevant (Curio, 1976; Endler, 1978; Krebs, 1978). Seasonal or temporal changes in availabiltiy of food, hunger and breeding patterns may also affect the selectivity of species or individuals (Curio, 1976). Individuals within a species were also shown to be significantly different in their prey preferences (see, for example, Chapters 4 and 5). These differences must be taken into consideration when comparisons between experiments are made and may aid in discussions of aberrant results. Observation of experiments is therefore obviously important and the use of a large number of individuals and replication of experiments are essential before any general conclusions can be made. My experiments were replicated and observed when practicable.

11.3 PROTECTIVE COLORATION AND CRYPSIS

The experiments have shown that the coloration of a prey can affect its chances of avoiding predation from visually hunting predators. Evidence was obtained to support the theory of crypsis: that the prey types with coloration that represented most closely the background in colour and pattern had the greatest probability of survival.

The birds could discriminate between very similar colour patterns. Coloration that produced a general resemblance to the background would confer an advantage to a prey animal over another prey animal that had no resemblance at all; but any genetic mutation which produced coloration that was a better match to the background, however similar to the original coloration, would be at a selective advantage (Cott, 1940; Endler, 1978). The outcome would be the perfection of crypsis by predator selection.

11.4 NOVELTY AND FAMILIARITY

Experiments using artificial prey, some of which were brightly coloured (Chapter 5), suggested that birds avoided novel prey types or preferred the familiar (or prey that most closely resembled the familiar) prey types. These two behaviours are distinct because they are responses to opposite prey types: either the familiar or the novel. A preference for familiar prey might only affect prey populations where there is a choice between two or more prey types, whereas avoidance of novel prey might result in prey not being eaten regardless of whether there were other prey types in the area.

11.4.1 Novelty

Many experiments have shown that young and inexperienced birds do not sample all prey items in an area; novel prey often do not elicit an attack response.

Rabinowitch (1965) raised two groups of chickens on two different monotonous diets. When the chicks were 42 days old each group was switched to the other group's diet. Half of the chicks did not sample the novel diet, and starved. Further studies (Rabinowitch, 1968) showed that chicks of the herring gull and the ring-billed gull preferred their training food to unfamiliar food, and that many did not respond at all when only unfamiliar food was presented to them. Other studies with chicks (Hogan, 1965) found that some naive birds would not attack mealworms when they were presented initially, and they also exhibited fear and escape behaviour when first presented with the mealworms.

Blue jays (*Cyanocitta cristata*), grackles (*Quiscalus quiscula*) and red-winged blackbirds (*Agelaius phoeniceus*) were used in a study testing the reactions of naive birds to novel insects (Coppinger, 1970). The birds had been taken from the nest prior to fledging and they were fed on cylindrical pigeon pellets and mealworms. The birds were then presented with novel food in the form of dead butterflies. The results confirmed that birds do not immediately attack all novel insects. Sixteen out of the thirty hand-raised birds had to be trained to eat a mealworm, and seventeen never touched any of the butterflies presented. These were not passive rejections.

The coloration of the novel prey may also be a factor affecting the response of the birds. Coppinger's birds were divided into two groups and each group received either a bright red and black butterfly (*Anartia amalthea* L.) or a brown and white butterfly (*A. jatrophae* L.). Both bird groups were inhibited in their attacks. Most of the group that received the brown and white butterflies habituated to the stimulus; the other group did not. The group that had habituated to the brown and white butterfly was then presented with the red and black butterfly. Most birds at first showed some inhibition from attacking it but did eventually. Coppinger believed that this difference in behaviour towards the red and black butterfly by each group could only have been a function of experience with the brown and white butterfly: in one group the naive birds proceeded from brown laboratory food and light brown mealworms to brown and white butterflies to red and black butterflies - each new stimulus had features in common with a previous one. The birds that had seen the red and black *A. amalthea* first were also inhibited from attacking the brown and white *A. jatrophea*, and the inhibition lasted for a longer period than that of the other group. Coppinger's hypothesis is that both the inhibition of attack and the strength of the response are a relationship between the amount of stimulus change and the past experience of the animal, and are not related to any particular characteristics of the stimulus *per se*. He does not think that the inhibition shown by the birds to attack the red and black butterfly was an innate fear of these colours. To test for this he should have carried out the reverse experiment of using, for example, red-coloured mealworms and pigeon pellets as training foods instead of the natural brown coloured foods he did select. Nevertheless, he has shown that novelty generally inhibits an attack response in naive birds.

These studies are relevant to the experiments reported in Chapter 5 because novelty of some (or all) of the prey types was an important factor. However, the above studies concerned young and naive birds whereas those of Chapter 5 used wild birds that were experienced predators. This difference could be important. All the birds that visited my experiments would have continually experienced new prey items during their lives.

Wild-caught blue jays were used by Coppinger (1969) in a similar series of experiments to those of his of 1970. He presented the jays with dead neo-tropical butterflies of which they could have had no experience. There were different training diets, ranging from varied to monotonous and from non-butterfly to butterfly. The experiments showed that the training diet had a significant effect on the birds' reactions to the test butterfly. The rejection of a novel butterfly was very seldom passive. In many cases, the bird approached the half-hidden cup expecting to find familiar food and upon sighting the new butterfly the bird would retreat to the farthest corner of the cage, sometimes giving an alarm call.

The concept of 'arousal' or 'level of activation' was used by Coppinger (1970) to explain inefficient attacks on novel insects by his blue jays. Arousal has been suggested as the state which is along a continuum from drowsiness to extremes of alertness and responsiveness (review of neurological studies in Hinde, 1970). A given stimulus causes interaction of physiological and behavioural events and results in a specific arousal level. The arousal level determines the ability of an animal to respond to a stimulus. Thus a frightened animal might be less capable than an alert animal of attacking a novel prey. There is the possibility that there are optimum limits of input for responsiveness, efficiency or performance, and there is evidence that there is a decrease in performance as the input increases beyond an optimum (Hinde, 1970). If a predator encountered a novel prey type that was only slightly different from a familiar prey type, the stimulus would cause less arousal in the predator than it would if the novel prey was substantially different. This suggests that any new morph which was very different in appearance from established morphs would be at an advantage from predation over new morphs which differed only slightly (called 'aspect diversity' by Rand, 1967). Distinct colour patterns between morphs may be one of the results of this advantage. Of course, the avoidance of morphs with new distinct colour patterns might be short-term as they become more familiar to predators. In having very different (or brighter) colour patterns, there may be disadvantages that would outweigh any advantage gained from an initial avoidance by predators: these would include a lack of intra-specific recognition or an increase in conspicuousness in edible prey. The initial aversion to brightly coloured and very distinct prey, for example those of Chapter 5, would be of particular value in the development of aposematic coloration.

11.4.2 Familiarity

Familiarity has also been shown to affect birds' responses to different prey types. Training experiments reported in Chapters 6 and 9 showed that wild garden birds (experienced predators) preferred the familiar of two prey types with different colour patterns when given the choice. Another training experiment (Chapter 8) attempted to test whether chicks preferred the prey type that was most similar to a familiar prey type and the results suggested that this prey type was at marginally greater risk from predation. Preference for the prey type which has been the most recently encountered is different in behavioural terms from an avoidance of novel food. In the 'reverse' training experiments, where the birds were trained on the second prey type, the subsequent choice test gave the birds prey types with which they had had previous experience. Yet they still preferred the prey type that they had been most recently trained on. This behaviour was different from the avoidance of novel prey because neither prey type was novel in the second choice test. The result of this behaviour might be particularly important in the natural situation where prey populations were spatially separate. An example would be where a predator moves from an area with only one prey type (or with a very high percentage of one prey type) to an area with a different proportion of prey types. The predator may preferentially feed on the prey type it had most recently been feeding on, or, if this prey type was not available, may choose the most similar prey type. The effect of this preference on the prey population would depend on the proportions of the prey types: if there was a high percentage of the familiar prey type, the result would appear to be apostatic selection; if the familiar prey type was rare, anti-apostatic selection would result. A similar effect could occur in prey populations separated by time, but this would depend on how long the preference lasted. The mechanism involved in the establishment of a preference will be an important factor.

If the prey are cryptic, then the establishment of a preference for a particular prey type might be the result of a search image (see Chapter 1, Section 1.4.3). Evidence has been provided for short-term search images (Dawkins, 1971a; Pietrewicz and Kamil, 1981; Lawrence, 1985a,b)[1]. If a search image only lasts for a short time then temporal or spatial difference between prey populations might preclude preferences being transferred from one prey population to another. There is evidence that blackbirds can retain search images from one feeding bout to another over a number of days (Lawrence, 1985b), but whether the search image would be retained between spatially separate populations has not been tested.

It is a possibility that the birds were 'learning to see' the first training prey type used in the training experiments reported in Chapters 6 and 9. For example, in Experiment 5a at Site 1, it took over 24 hours before the plain green training prey were fed on for the first time; and the birds had had to be lured to the area with white pastry. At Sites

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[1] These experiments have been criticised by Guilford and Dawkins (in press), who attribute any increased ability in the detection of cryptic prey to predators slowing their search rate.

2, 3 and 4, also, white pastry had to be scattered at the commencement of the experiments when it became apparent that the prey were untouched. At Site 5, the white pastry was also untouched for the first two days. However, predation on the red-striped green prey occurred almost immediately at Site 6. Similar delays in initial predation occurred in Experiment 5b, Site 2 (Site 1 was also used in Experiment 5a and in other experiments; therefore the birds were used to feeding on the experimental prey), and in Experiment 5c. Of course it is possible that the birds may not have recognised the pastry prey as potential prey or that they were avoiding novel food, as already discussed. In Experiment 10 (Chapter 9), where pastry-filled snail shells were used as the prey, a choice test preceded the training period: predation at Site 1 first occurred over 24 hours after the shells were put out; and at Site 2 (Site 6 of Experiment 5a) the shells were first pecked after eighteen minutes. If a search image was acquired for the training prey type in these experiments then the subsequent preferences for these prey could be explained by this mechanism. The preferences lasted, with no apparent reinforcement, over the three day post-training choice tests of Experiments 5a and 5c. Allen (1974) also found persistent preferences for the training prey type over three days, but his prey were not meant to be cryptic and therefore the acquisition of search images by the birds was probably not an issue in his experiments. Whatever the mechanism(s), in my experiments the birds preferred the prey type that they had most recently been feeding on and this behaviour also occurred with prey types that were similar (see also Allen, 1984).

The opposite response to that observed in the other training experiments was found in a further experiment using prey that differed slightly in their colour patterns (Chapter 7): there was a decrease in the proportion of the familiar prey type eaten over the course of time in the first experimental series where the training prey type was the same throughout. One suggestion for this result is that the birds were choosing a mixed diet. Further implications of these results are discussed in the next section.

11.5 FREQUENCY-DEPENDENT SELECTION AND POLYMORPHISM

As discussed above, if predators either prefer prey with familiar colour patterns or avoid prey with novel colour patterns, or if there is a mixture of both in the behaviour of predators, the result may be the initial survival of new prey colour patterns. However, only a preference for familiar colour patterns might result in the maintenance of a colour pattern polymorphism since rare morphs will not remain novel to predators because they will be encountered sooner or later, however infrequently. Training experiments (Chapters 6 and 9) have shown that a preference for a colour pattern may be reversed after exposure to monomorphic populations of the unfamiliar prey type, and this implies that bird predators could respond to fluctuations in relative morph frequencies by changing their preferences to whichever prey colour pattern was the most common. The significance of these results is that the preferences of the birds can be based on striped colour patterns - common in many polymorphic species (see Section 1.5, Chapter 1).

The results from the training experiments on grass indicated that, as the prey types increased in similarity, there was a decrease in the strength of the training response. Thus, in Experiments 5a, 5b and 5c, reported in Chapter 6, the strongest training response occurred in Experiment 5a where the two prey types differed in the presence or absence of a red stripe; whereas in Experiments 5b and 5c the stripe was green and, since the ground colour of the prey was a similar colour green, the two prey types were less distinct. The results from the training response found in Experiment 7, Chapter 7, also appeared to indicate that the strength of the training response decreases as the prey types increase in similarity (but see also the subsequent discussion of Experiment 7). An alternative explanation for the differences in training response between Experiments 5a, 5b and 5c, is that they were affected by the differences in conspicuousness between the two types of striped prey: more conspicuous prey types elicited a stronger training response, and, from the results of Experiments 2 and 3, Chapter 4, the red-striped prey type was the most conspicuous. This alternative explanation would conflict with the conclusions of Cooper (1984b) that apostatic selection in his experiments was stronger when the prey were cryptic than when they were conspicuous (see also Bond, 1983). Clarke (1962) and Greenwood (1984) both predict that frequency-dependent selection should decrease with increased crypsis because predators would be less likely to discriminate between the morphs. In the training experiments of Allen (1974), both the brown and green pastry prey were conspicuous on the grass background, and there were many feeding bouts in which only the training prey type was eaten. However, Allen (1984) found that in his training experiments with similar prey (a range of prey which consisted of the brown and green prey used previously together with a series of intermediates) the effects of training were decreased in comparison with those of the 1974 experiments. Therefore it is not clear whether the observed difference in training response between the red-striped and the green-striped prey types was the result of the difference in similarity or because of the difference in crypsis of the two prey types. If apostatic selection is stronger on prey that match their backgrounds (Cooper, 1984b) then this effect would have been to increase the training response, whereas the effects of increasing similarity would have decreased the training response (Allen, 1984).

Another interesting possibility that arose from the training experiments on striped and unstriped prey was that the training response was stronger after training on striped rather than plain prey, and this was seen in Experiments 5a and 5b where there were significantly higher proportions of striped prey taken in the striped-trained experiments than plain prey in the plain-trained experiments. However, in Experiment 5c, there was a tendency for the plain prey in the plain-trained experiments to be taken in a higher proportion than striped prey in the striped-trained experiments, although this difference was very small (and statistically insignificant, Site 1: $p>0.5$; Site 2: $p>0.8$). If it were the case that birds generally formed a stronger preference for familiar striped (or patterned) prey than for plain prey, then, in a polymorphic population, patterned prey might be at a relative disadvantage. Of course, there might be other advantages in being patterned, such as increased crypsis. However, if being striped or patterned did not confer an advantage in crypsis, then it could be predicted that any polymorphism regarding coloration would be based around different ground colorations rather than around different patterns on one ground colour. If the strength of a preference for a familiar prey type was decreased as the prey types increased in similarity (see discussion above) then it would be predicted that the prey type that was the most distinct from the familiar (common) morph would be at a selective advantage. Thus, within the constraints of selection for crypsis (and climatic and intra-specific selection) these other aspects of visual selection by birds might result in a polymorphism based around plain colours that were quite distinct from each other.

The training experiments of Chapter 7 seemed to indicate either that the birds could not distinguish between the prey colour patterns used or if they did training them on one prey type did not result in overpredation of the training prey type. In the first series, where the training prey type was the same for each experiment, a decrease in the proportion of the training prey type over the series of experiments was observed. This behaviour would not maintain a polymorphism since predators would start to prefer the unfamiliar (rarest) prey type after preferring the familiar prey type (most common) in a population. Past training experiments (eg. Croze, 1970; Allen and Clarke, 1968; Allen, 1973, 1974, 1984; Raymond, 1984) have not lasted long enough to ascertain if there is this trend in the birds' preferences in the course of time. If there has been a change, as in, for example, a move towards an equal choice of the two prey types in the 1:1 populations, the assumption has been that there has been a waning of the training response (Allen, 1973). The 1:1 populations were not presented for more than one to three days after training. If these populations were presented over a longer period of days, the results from the first series of Experiment 7 suggest that one predicted outcome might be that the birds would start to avoid the familiar (training) prey type and would overpredate the unfamiliar prey type. An experiment that could study this response further would be to present 9:1 populations to the same birds repeatedly at a prey density of perhaps $2/m^2$ to see if there was a change from apostatic to anti-apostatic selection. It is possible that the preference of the birds for the common prey type (or familiar) is only an initial (or short-term) response; if this were shown to be so, then the experimental evidence for frequency-dependent selection maintaining polymorphisms needs to be reassessed. An alternative explanation is that the results from the first series in Experiment 7 were due to the prey types being very similar in their colour patterns and that a stronger or more long-term training response would result if the prey types were more distinct (Clarke, 1962; Allen, 1984). If this were the case, then, in a species polymorphic for colour patterns, and within the constraints of climatic and sexual selection, there may be selection for the morphs to be quite distinct from each other (Clarke, 1962; Greenwood, 1984).

The experiments using a range of prey frequencies (Chapter 10) showed that, with no training, birds can select for or against a striped colour pattern in a frequency-dependent manner. It was found that, at the two higher densities, the birds preferred the rarer prey type, the ultimate result of which would be a monomorphic prey population. Possible reasons for this anti-apostatic selection are discussed in detail in Section 10.4 (Chapter 10) but can be summarised here. Predators may choose the 'odd' prey type in groups of prey because it might be easier to concentrate on this prey type when there are many prey in the sensory field at any one time (Greenwood, 1984). At the 'maximum' prey density, birds may choose the rare prey type because it 'stands out' from the background of the common prey types (Allen, 1972). These explanations are easier to apply to the extreme prey frequencies such as 1:9 and 9:1, but it is interesting to note that, at the prey density of $30/m^2$ when the numbers of each prey type in the population were 18 and 42 (prey frequency 3:7), the birds still preferred the rarer prey type (Appendix to Chapter 10), and this was particularly clear at Site 1, Experiment 9a where a paired comparison of the β_Ts obtained for 3GR:7G and 7GR:3G was highly statistically significant ($F_{(1,8)} = 26.803$, $p<0.001$). At this prey frequency it is difficult to see why the birds should have preferred the rarer prey type unless the birds responded to even this difference in prey numbers. Allen and Anderson (1984) suggest that anti-apostatic selection is the result of bird predators concentrating on one prey type during feeding bouts at 'high' prey densities; however, observation in my experiments did not show this type of feeding behaviour.

11.6 PREY DENSITY

The effects of density in individual experiments have been discussed individually in the relevant chapters but some general points can be made here. The density of the prey populations has been shown to affect the choice of prey types by birds. In the choice tests described in Chapter 4, the birds were more selective at the prey density of $30/m^2$ (Experiment 2) than at the prey density of $1/4m^2$ (Experiment 3). In the experiments reported in Chapter 10 (Experiments 9a, 9b and 9c), in which the prey frequencies were changed, the density of the prey affected the direction (and probably the strength) of frequency-dependent selection (Cook and Miller, 1977; Willis *et al.*, 1980). With my prey types, the prey density of $30/m^2$ was found to be a density where the birds were very selective (Experiment 2: **GR>G>GG**); therefore it was consistent that strong selection was found at this density in Experiment 9a. Birds were also selective after training at the density of $2/m^2$ (Experiments 5a, 5b and 5c, Chapter 6), but were not shown to be selective in Experiment 9c. Similarly, birds were selective at the prey density of $1/4m^2$ in the choice tests of Experiment 3 (**GR>G>GG**) but not in Experiment 9c at this density. No experiments other than those reported in Chapter 10 were done at the 'maximum' prey density of $3850/m^2$, therefore the effects of different experimental designs cannot be compared.

All of the above experiments used prey of the same size and included prey types that were designed to be difficult to see on a grass background. Direct comparisons with experiments by other workers are not strictly possible because of the many variables involved, such as prey size and relative conspicuousness. The prey densities at which frequency-dependent selection occurs and the strength of any selection may be dependent on prey size and differences in prey coloration. Different degrees of similarity between prey types in populations may also result in different outcomes at the same prey densities. The different predators used may also dictate the occurrence and direction of any visual selection (see Section 11.2). There are many variables that have to be taken into account in the prediction or explanation of any visual selection and differences in these factors may also explain why there are not always consistent trends in different prey populations and in different experiments.

11.7 SUGGESTIONS FOR FUTURE WORK

The work presented in this thesis has demonstrated that birds often select their prey on the basis of coloration and that this selection can be frequency-dependent.

The responses of wild birds to different colour patterns of artificial prey can be studied. For example: comparisons could be made between prey types with different numbers of stripes; the colours or direction of striped patterns could be changed. Choice tests, training experiments and experiments across a range of prey frequencies could all be used to investigate the effects of these different colour patterns.

Other areas for future work which are not necessarily specific to prey colour patterns have also emanated from results from my experiments, and those of greatest interest are listed below. In particular, those areas suggested by paragraphs 2, 3 and 5 would be directly relevant to natural populations.

1. The training periods used in training experiments by all workers have been chosen arbitrarily and the length of this period may affect the strength of any post-training preferences. Different training periods may be necessary with different prey types. For example, prey types that are very similar may need to be presented for a longer period than prey types that are very distinct before predators exhibit any preferences. This could be tested with a series of experiments using different training periods with pairs of prey types that vary in respect to similarity. The length of time that any preferences persist may also be affected by the length of training period and also by the degree of similarity of prey types, therefore the post-training 1:1 populations could be presented over a relatively long period of time (see also next paragraph).

2. The results from Experiment 7 suggested the possibility that preferences found for familiar or common prey types is a short-term response and Section 11.5 of this chapter contains the suggestion that experiments could be performed to investigate whether this is true. The experiment proposed is that birds should be presented with populations of prey types at the frequency of 9:1, over a long period of time (compared with previous experiments), to see if there is a change from apostatic to anti-apostatic selection.

3. Experiments based on the design of Experiment 4 (Chapter 8) could be performed using wild predators to establish whether, after feeding on a monomorphic population (or on a common prey type), they prefer the prey type that is most similar to the familiar prey type. The design could be modified to include studies of the effects of different simlilar prey types in adjacent prey populations.

4. Although the results from Experiment 10 (Chapter 10) showed that training birds on unbanded or five-banded pastry-filled *Cepaea hortensis* shells affected the birds' subsequent choices of the two shell types, the bird species that were the predators were not those that would be the predominant predators of *Cepaea* in the wild. Therefore, although the behaviour shown by the blackbird and sparrows of Experiment 10 is e vidence for potential frequency-dependent selection by these species of birds, there is no evidence that it would substantially affect the natural polymorphic species *Cepaea*. Ideally, further replicates of this experiment with natural predators of *Cepaea* (i.e., song thrushes) are desirable.

5. Further behavioural studies are also needed in the areas of selection against conspicuous forms and frequency-dependent selection.

The use of artificial prey has proved to be valuable in the research on the effects of prey coloration and lends itself to many further studies; however, as has always been the case, studies using real prey types and their natural predators should be made whenever possible.

11.8 CONCLUDING REMARKS

The function of animal coloration in defence against predators has been the subject of discussion for over a hundred years (Poulton, 1890; Cott, 1940; Tinbergen, 1957; Robinson, 1969; Edmunds, 1974; Endler, 1978). One question has been whether coloration that appeared to act as camouflage is the result of selection by predators or whether it was just an 'accident of nature'. Many prey species that are polymorphic for coloration also appear to be cryptic. It has been suggested that predators may select colour patterns in a frequency-dependent manner and thereby maintain such colour pattern polymorphisms (Poulton, 1884; Clarke, 1962).

I chose to use striped colour patterns to investigate protective coloration and frequency-dependent selection. The results of my experiments have shown that birds can discriminate between very similar colour patterns, that they can select on the basis of colour patterns and that this selection can be frequency-dependent.

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GENERAL APPENDIX A

Examples of BBC BASIC computer programs
for determining prey distributions.

Program in BBC BASIC for determining random distribution of prey in Experiment 7, Chapter 7.

```
  5 X=RND(TIME):Y=RND(-X)
 10 REM DISTRIBUTION OF 6 PREY
 20 VDU2
 30 PRINT "EXPERIMENT 7:  CONTROL EXPT."
 40 PRINT
 50 PRINT "SITE:  BOLDREWOOD"
 60 PRINT
 70 PRINT "DATE:"
 80 PRINT
 90 PRINT "WEATHER:"
100 PRINT
110 PRINT
120 PRINT
130 PRINT
140 MODE 4:VDU3
150 CLS
160 VDU 23,250,124,146,146,146,146,146,146,124
170 VDU 23,240,124,146,146,130,130,146,146,124
180 VDU 23,230,124,186,186,186,186,186,186,124
190 VDU 23,220,124,138,138,138,138,138,138,124
200 VDU 23,210,124,130,130,254,254,130,130,124
210 VDU 23,200,124,214,214,214,214,214,214,124
220 LET A=2:B=10:C=2:D=10
230 GOSUB 890
240 LET A=14:B=22:C=2:D=10
250 GOSUB 890
260 LET A=2:B=10:C=14:D=18
270 GOSUB 570
280 LET A=14:B=22:C=14:D=18
290 GOSUB 570
300 PRINT TAB(32,1);"START:"
310 PRINT TAB(31,2);"FINISH:"
320 PRINT TAB(31,5);"Nos Taken"
330 PRINT TAB(35,7);CHR$(250)" ="
340 PRINT TAB(35,9);CHR$(240)" ="
350 PRINT TAB(35,11);CHR$(230)" ="
360 PRINT TAB(35,13);CHR$(220)" ="
370 PRINT TAB(35,15);CHR$(210)" ="
380 PRINT TAB(35,17);CHR$(200)" ="
390 PRINT TAB(35,19);"T ="
400 PRINT TAB(2,22);1
410 PRINT TAB(6,22);2
420 PRINT TAB(10,22);3
430 PRINT TAB(14,22);4
440 PRINT TAB(18,22);5
450 PRINT TAB(22,22);6
460 PRINT TAB(26,2);"A"
470 PRINT TAB(26,6);"B"
480 PRINT TAB(26,10);"C"
490 PRINT TAB(26,14);"D"
500 PRINT TAB(26,18);"E"
510 GOSUB 1210
520 *SAVE SCREEN 5800 7500
```

```
 530 IF GET$=" " GOTO 540 ELSE GOTO 560
 540 *pdump
 542 *FX18
 545 GOTO 530
 550 PRINT TAB(0,30);" "
 560 END
 570 J=0:K=0:L=0:M=0:N=0:O=0
 580 X=0: Y=0
 590 FOR F=A TO B STEP 4
 600 FOR G=C TO D STEP 4
 610 FOR S=1 TO 2
 620 P=X:Q=Y
 630 LET X=(SGN(RND(1)-0.5))+F
 640 LET Y=(SGN(RND(1)-0.5))+G
 650 IF X=P AND Y=Q THEN GOTO 630
 660 LET R=RND(6)
 670 IF R=1 AND J=2  GOTO 660
 680 IF R=2 AND K=2  GOTO 660
 690 IF R=3 AND L=2  GOTO 660
 700 IF R=4 AND M=2  GOTO 660
 710 IF R=5 AND N=2  GOTO 660
 720 IF R=6 AND O=2  GOTO 660
 730 IF R=1 THEN LET J=J+1
 740 IF R=2 THEN LET K=K+1
 750 IF R=3 THEN LET L=L+1
 760 IF R=4 THEN LET M=M+1
 770 IF R=5 THEN LET N=N+1
 780 IF R=6 THEN LET O=O+1
 790 IF R=1 PRINT TAB(X,Y); CHR$(250)
 800 IF R=2 PRINT TAB(X,Y); CHR$(240)
 810 IF R=3 PRINT TAB(X,Y); CHR$(230)
 820 IF R=4 PRINT TAB(X,Y); CHR$(220)
 830 IF R=5 PRINT TAB(X,Y); CHR$(210)
 840 IF R=6 PRINT TAB(X,Y); CHR$(200)
 850 NEXT S
 860 NEXT G
 870 NEXT F
 880 RETURN
 890 J=0:K=0:L=0:M=0:N=0:O=0
 900 X=0: Y=0
 910 FOR F=A TO B STEP 4
 920 FOR G=C TO D STEP 4
 930 FOR S=1 TO 2
 940 P=X:Q=Y
 950 LET X=(SGN(RND(1)-0.5))+F
 960 LET Y=(SGN(RND(1)-0.5))+G
 970 IF X=P AND Y=Q THEN GOTO 950
 980 LET R=RND(6)
 990 IF R=1 AND J=3  GOTO 980
1000 IF R=2 AND K=3  GOTO 980
1010 IF R=3 AND L=3 GOTO 980
1020 IF R=4 AND M=3  GOTO 980
1030 IF R=5 AND N=3  GOTO 980
1040 IF R=6 AND O=3  GOTO 980
1050 IF R=1 THEN LET J=J+1
1060 IF R=2 THEN LET K=K+1
```

```
1070 IF R=3 THEN LET L=L+1
1080 IF R=4 THEN LET M=M+1
1090 IF R=5 THEN LET N=N+1
1100 IF R=6 THEN LET O=O+1
1110 IF R=1 PRINT TAB(X,Y); CHR$(250)
1120 IF R=2 PRINT TAB(X,Y); CHR$(240)
1130 IF R=3 PRINT TAB(X,Y); CHR$(230)
1140 IF R=4 PRINT TAB(X,Y); CHR$(220)
1150 IF R=5 PRINT TAB(X,Y); CHR$(210)
1160 IF R=6 PRINT TAB(X,Y); CHR$(200)
1170 NEXT S
1180 NEXT G
1190 NEXT F
1200 RETURN
1210 MOVE 16,1008
1220 DRAW 16,368
1230 DRAW 784,368
1240 DRAW 784,1008
1250 DRAW 16,1008
1260 MOVE 16,496:DRAW 784,496
1270 MOVE 16,624:DRAW 784,624
1280 MOVE 16,752:DRAW 784,752
1290 MOVE 16,880:DRAW 784,880
1300 MOVE 144,368:DRAW 144,1008
1310 MOVE 272,368:DRAW 272,1008
1320 MOVE 400,368:DRAW 400,1008
1330 MOVE 528,368:DRAW 528,1008
1340 MOVE 656,368:DRAW 656,1008
1350 PRINT TAB(31,24);" "
1360 RETURN
```

Program in BBC BASIC for determining random distribution of prey in Experiment 9c, Chapter 10.

```
 10 X=RND(TIME):Y=RND(-X)
 20 REM G AND GR CHANGE FREQUENCIES AND DENSITES
 30 PRINT "INPUT FREQUENCIES"
 40 INPUT FREQ$
 50 PRINT "INPUT TOTAL NUMBER OF EACH PREY TYPE"
 60 INPUT NUMB$
 70 PRINT "INPUT TRIAL NUMBER"
 80 INPUT T
 90 VDU 2
100 PRINT "EXPERIMENT 9c - CHANGE IN FREQUENCIES AND DENSITES"
110 PRINT
120 PRINT "SITE: BOLDREWOOD"
130 PRINT
140 PRINT "FREQUENCIES:  ";FREQ$
150 PRINT
160 PRINT "TOTAL NUMBER OF EACH PREY TYPE:  ";NUMB$
170 PRINT
180 PRINT "DATE"
190 PRINT
200 PRINT "WEATHER:"
210 PRINT
220 PRINT "TRIAL:  ";T
230 PRINT
240 PRINT
250 PRINT
260 MODE4:VDU3
270 VDU 23,190,124,130,130,130,130,130,130,124
280 VDU 23,250,124,146,146,146,146,146,146,124
290 CLS
300 A=2:B=22:C=2:D=18
310 GOSUB 560
320 PRINT TAB(32,1);"START:"
330 PRINT TAB(31,2);"FINISH:"
340 PRINT TAB(31,5);"Nos Taken"
350 PRINT TAB(35,7);CHR$(190)" ="
360 PRINT TAB(35,9);CHR$(250)" ="
370 PRINT TAB(35,12);"T ="
380
390 PRINT TAB(2,22);1
400 PRINT TAB(6,22);2
410 PRINT TAB(10,22);3
420 PRINT TAB(14,22);4
430 PRINT TAB(18,22);5
440 PRINT TAB(22,22);6
450 PRINT TAB(26,2);"A"
```

```
460 PRINT TAB(26,6);"B"
470 PRINT TAB(26,10);"C"
480 PRINT TAB(26,14);"D"
490 PRINT TAB(26,18);"E"
500 PRINT TAB(31,24);" "
510 GOSUB 710
520 IF GET$=" " GOTO 530 ELSE END
530 *pdump
540 *FX18
550 END
560 O=0:T=0
570 X=0:Y=0
580 FOR M=A TO B STEP 4
590 FOR N=C TO D STEP 4
600 FOR S=1 TO 2
610 P=X:Q=Y
620 LET X=(SGN(RND(1)-0.5))+M
630 LET Y=(SGN(RND(1)-0.5))+N
640 IF X=M OR Y=N THEN GOTO 620
650 IF X=P AND Y=Q THEN GOTO 620
660 PRINT TAB(X,Y);CHR$(190)
670 NEXT S
680 NEXT N
690 NEXT M
700 RETURN
710 MOVE 16,1008
720 DRAW 16,368
730 DRAW 784,368
740 DRAW 784,1008
750 DRAW 16,1008
760 MOVE 16,496:DRAW 784,496
770 MOVE 16,624:DRAW 784,624
780 MOVE 16,752:DRAW 784,752
790 MOVE 16,880:DRAW 784,880
800 MOVE 144,368:DRAW 144,1008
810 MOVE 272,368:DRAW 272,1008
820 MOVE 400,368:DRAW 400,1008
830 MOVE 528,368:DRAW 528,1008
840 MOVE 656,368:DRAW 656,1008
850 RETURN
```

GENERAL APPENDIX B

Published Paper

Raymond, D.L. (2008) **Wild birds prefer the familiar of striped and unstriped artificial prey** The Biological Journal of the Linnean Society: 23 (2-3), 229-235 https://doi.org/10.1111/j.1095-8312.1984.tb00141.x