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PREDATION ON POLYMORPHIC PREY: THE EFFECTS AND BEHAVIOURAL BASES OF FREQUENCY-INDEPENDENT AND FREQUENCY-DEPENDENT SELECTION

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To my Parents

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ABSTRACT

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PREDATION ON POLYMORPHIC PREY: THE EFFECTS AND BEHAVIOURAL BASES OF FREQUENCY-DEPENDENT AND FREQUENCY-INDEPENDENT SELECTION

by Graham Michael Tucker

Apostatic selection (frequency-dependent selection by predators) has been demonstrated in several studies and theoretical work indicates that it has the potential to maintain polymorphism. Although apostatic selection has been proposed as a process that may help maintain colour polymorphisms in molluscs such as *Cepaea* and *Littorina* there is little evidence to support this. The underlying behavioural basis of apostatic selection is also poorly understood. The experiments described in this thesis attempted to establish: (1) whether predators exert frequency-independent visual selection on visually polymorphic molluscs and which factors affect the degree and direction of selection, (2) whether predators could exert apostatic selection on artificial populations of *Cepaea* and *Littorina*; (3) the behavioural mechanism underlying apostatic selection.

A two year field study of snail predation by song thrushes (*Turdus pilomelos*) revealed selection on the colour morphs of *Cepaea*. During the winter yellow five-banded morphs were at a selective advantage and pink unbanded at a disadvantage. Yellow five-banded morphs were also at a selective advantage in the summer as were yellow unbanded morphs, whilst morphs with fused bands were at a disadvantage. No significant changes in selection were observed in either predation period.

An experiment was carried out to test whether captive song thrushes would feed in an apostatic manner on an artificial dimorphic population of *Cepaea*. Although the results gave some indication that selection was frequency-dependent they were not conclusive, because of the small number of replicates.

Another experiment tested whether shore crabs (*Carcinus maenas*) exert frequency-independent visual and/or apostatic selection on an artificial dimorphic population of *Littorina mariae*. The results indicated that there was no visual or apostatic selection.

Some potential behavioural mechanisms causing apostatic selection were investigated using humans as ´predators´. In the first series of experiments ´populations´ of dimorphic ´prey´ (at one of seven frequencies) were presented on the screen of a computer colour monitor to subjects who were asked to use a light pen to remove each prey they detected. Each subject either had the prey presented against a matching background or against a background that made them conspicuous. The results showed that apostatic selection occurred, but only when the prey were inconspicuous. The results also showed that the apostatic selection was caused by some aspect of the subjects´ searching behaviour. Further experiments revealed that the overall degree of selection decreased with increasing density, although the individual effects on the frequency-dependent and frequency-independent components could not be established.

A second series of computer trials explicitly tested whether humans formed search images or modified their search rate when searching for cryptic prey images. In these experiments cryptic prey were presented singly amongst a series of blank screens and the subjects only had to detect whether a prey item was present. The results showed that the subjects did modify their search rate and this improved their ability to detect the prey. However, apostatic selection occurred when the prey were presented in unequal frequencies and this suggests that search images were formed.

CHAPTER 1

GENERAL INTRODUCTION

DISCONTINUOUS VARIATION OF VISUAL CHARACTERS AND SELECTION BY PREDATORS.

Discontinuous variation in the form of stable genetic polymorphisms (*sensu* Ford 1940) is widespread in the animal kingdom and has received much attention from ecological geneticists. Many investigations have centred on the question of why such polymorphisms are maintained, as the ´Darwinian´ concept of directional natural selection predicts the survival and predominance of a single fittest form, resulting in monomorphism. Although polymorphism occurs down to the molecular level, it is the maintenance of visual forms of discontinuous variation that I am concerned with here. In particular, my concern is the role of apostatic selection by predators in the maintenance of such polymorphisms.

Of such polymorphisms perhaps the most striking are those of the prosobranch and pulmonate molluscs, involving the colour and banding patterns of the shell and body. These animals have several aspects of their biology that are advantageous for the study of the maintenance of balanced polymorphisms and have therefore received considerable attention (for reviews see Jones, Leith & Rawlings 1977; Clarke *et al*. 1978; Cain 1983; Goodhart 1988). Although I shall consider the general role of apostatic selection in the maintenance of visual polymorphisms (and it´s underlying behavioural basis), the appraisal of its effect in natural predator/prey systems will concentrate on those cases involving molluscs.

DISCONTINUOUS VARIATION OF VISUAL CHARACTERS IN MOLLUSCS AND EVIDENCE FOR SELECTION BY PREDATORS

Evidence for natural selection on visual characters in terrestrial pulmonates

About 30% of the terrestrial landsnails of the British Isles are polymorphic for colour and pattern. Of these, many are found in the family Helicidae, and some common examples of these are listed in Table 1.1 (adapted from Clarke *et al.* 1978). The most frequently observed colours range from white through yellow, orange and red to brown. These background shell colours may be combined with darker bands of brown to black, running parallel to the shell whorls. Although these bands are often arranged on a pentateaniate theme, modifications are not uncommon: bands are lost or fused in various combinations. Throughout this thesis I shall refer to the visual polymorphisms of *Cepaea* using the conventional terms and criteria for the scoring of morphs as used by Cain & Sheppard (1950, 1954) and Clarke (1960). The morph colour referred to is always the underlying ground colour of the shell and not the bands. Bands are numbered from 1 to 5, from the top of the whorl downwards, and fused bands are recorded within brackets (eg. (123)45). Missing bands are denoted by 0. Unless otherwise stated, ´five-banded morphs´ are snails with five complete, fully pigmented and unfused bands (i.e. 12345).

Most of the evidence that snails are subject to selective predation comes from work with *Cepaea*. For example , glow-worms (*Lampyris noctiluca*) apparently select *Cepaea nemoralis* on the basis of their appearance, yellow and brown unbanded snails being selected in preference to yellow five banded (O´Donald 1968). Visual selection by predators favouring cryptic forms has been demonstrated in rabbits (*Oryctolagus cuniculus*) preferentially selecting conspicuous shells on the basis of tone (Cain 1953). However, in Britain probably the major predator exerting visual selection upon land snails, and certainly the most studied, is the song thrush (*Turdus philomelos*).

Indirect evidence that song thrushes exert visual selection on polymorphic landsnails has been provided by studies showing ´habitat correlations´ in *Cepaea*. Cain & Sheppard (1950), in a

Table 1.1. Some examples of colour polymorphism in the Helicidae, (adapted from Clarke *et al.* 1978).

SPECIES	DESCRIPTION
Helix aspersa (Mull.)	Red ground-colour of juvenile shell dominant to yellow; banded 12345* dominant to 10005; full pigment dominant to reduced pigment (*exalbida*). Source: Cook (1969).
Polymita picta (Born)	Polymorphic for colour, banding and striation. Shell, bands and striations can be brown, red, white or black. Other species of Polymita also highly polymorphic. Source: Torre y Huerta (1950) cited in Clarke *et al.* (1978).
Arianta arbustorum (L.)	Brown shell dominant to absence; mottled shell dominant to unmottled; pigmented band dominant to unpigmented; white opaque stripe dominant to absence of stripe. Source: Cook & King (1966).
Cepaea nemoralis (L.)	Highly polymorphic. An allelic shell-colour series from brown to pale yellow, darker colours dominant to paler; unbanded dominant to banded; punctate bands dominant to unmodified; ´spread´ bands dominant to unmodified; normal bands and lip dominant to hylazonate bands and white lip. All these loci linked. Six other loci (2 controlling suppression of particular bands, and others controling orange bands, dark bands, colour of body, and quantity of dermal pigment) are known. Source: Many authors reviewed by Murray (1975).
Cepaea hortensis (Mull.)	Polymorphism very similar to that of *C. nemoralis*. Four linked loci known (controlling shell-colour, presence or absence of bands, pigmentation of bands and punctate bands). Source: Many authors reviewed by Murray (1975).
Monacha cantiana (Montagu)	Dark mantle colour probably dominant to light. Source: Cain (1971).
Theba pisana (Mull.)	Complicated polymorphism for shell-banding, perhaps variation on a pentateniate pattern. Source: Sacchi (1955).

* Bands are conventionally numbered 1 to 5 from the top of the whorl downwards. Zeros denote the absence of a particular band.

study near Oxford, demonstrated a close relationship between the ratios of colour and banding patterns in colonies of *Cepaea nemoralis* and the visual properties of the background on which they lived. Colonies in beechwoods with dark and uniform backgrounds usually contained high frequencies of brown and pink unbanded shells. Habitats with lighter and more variegated vegetation such as hedgerows and downland had high proportions of yellow and banded morphs. Cain & Sheppard interpreted these results as evidence that the predators exerted directional selective pressures on the polymorphic populations. As a result of these findings they recommended the reappraisal of polymorphic situations supposedly caused by drift. Further work by Cain & Sheppard (1952), Cain and Sheppard (1954), Currey, Arnold & Carter (1964), Cameron (1969b) and Greenwood (1974) has found similar correlations in other areas.

Cepaea hortensis also shows correlations between morph frequency and background (Clarke 1960). Dark cryptic morphs occur at high frequencies in woodland habitats, as in *Cepaea nemoralis*. However, the dark *Cepaea hortensis* morphs are five banded yellows that are cryptic because of the fusion of their bands which conceals their lighter underlying shell colour. Colonies in grasslands have high proportions of light unbanded shells and those in hedgerows have high frequencies of banded shells lacking fusions. Similar associations between morph frequency and habitat type in *Cepaea hortensis* were found in later studies by Cameron (1969b) and Greenwood (1974).

Song thrushes break open the shells of snails by hitting them against nearby stones (termed 'anvils'), and thus it is possible to monitor the birds selection by examining the shell remains and comparing the frequencies eaten with the frequencies in the available population. Lamotte (1950) first used this technique to obtain direct evidence that predation by thrushes resulted in differential selection of the morphs according to their visibility. However, he later concluded that the selective effects of the thrushes were negligible, arguing that song thrushes in France feed on snails primarily in the winter when they are buried, and therefore visual cues are not used to detect them. However, later studies by many workers have shown that these conclusions were ill-founded. Sheppard (1951) in a detailed study involving the release of marked snails showed that thrushes preferentially selected yellow morphs from a population of *Cepaea nemoralis*. He also showed that the percentage of yellow snails killed decreased from the middle of April to the middle of May. Sheppard interpreted this change to be a consequence of the background colours becoming greener during this period, because he could show that the thrushes had not changed their feeding areas, nor was their any indication that the frequency of yellow shells in the feeding areas had decreased.

Goodhart (1958), in a study of *Cepaea hortensis*, found a similar increase in selection of pink shelled morphs in summer. However, the possibility that the change in selection was caused by changes in feeding behaviour by the thrushes could not be ruled out. Even small shifts of feeding location could give spurious evidence of natural selection, because significant changes in gene frequency may occur over distances less than 10 m (Clarke *et al.* 1978). This problem was overcome in a study by Wolda (1963) in which he monitored a marked population of *Cepaea nemoralis* until late summer. As in Sheppard´s (1951) study, the percentage of yellow unbanded morphs taken decreased at first, but then increased again later in the summer, demonstrating that yellow were once again at a disadvantage. Wolda suggested that the thrushes might have changed their preferences through experience with other prey, or that changes in behaviour of the morphs might have been occurring. Although these factors could not be ruled out, Carter (1968a) argued that the background colour change could still account for fluctuations in selection of the colour morphs, because in late summer the background at ground level was once again dark, because of shading from the fully grown dense vegetation. Carter had observed this in his repetition of the experiment of Sheppard (1951), when he found (like Wolda (1963)) that yellow unbanded morphs were taken preferentially in late summer.

Arnold (1966) established an artificial colony of *Cepaea nemoralis* to investigate selection of morphs by song thrushes on a background of beech litter. The background did not change in colour during the summer and he found a steady selection against the yellow morphs which did not change with season. This provides further evidence that the fluctuations in selective values of the colour morphs observed in other studies is a result of change in background colour.

Several studies have looked for direct evidence of selection on the banding component of the polymorphism in *Cepaea*. Of these, Sheppard (1951); Carter (1968a); Cain & Currey (1968) found no evidence of selection by thrushes. Although Lamotte (1950) and Cain & Sheppard (1954) claimed to have found differential selection of banded morphs, they did not use marked snails. As Clarke *et al.* (1978) point out "the live populations sampled may not have been exactly the same as those which the thrushes were hunting". However, studies by Wolda (1963) on *Cepaea nemoralis* and Bantock (1971) on *Cepaea hortensis* did use marked snails. Wolda found that the selection of banded individuals taken by thrushes changed significantly with season and Bantock showed that effectively fused morphs (i.e. those with fusions on the upper part of the shell, and therefore visible when viewed from above) were at a selective advantage when on a dark background in dense vegetation. However, Clarke *et al.* (1978) also criticise these studies on the grounds that the populations were established with different morphs from different colonies. Variations in the behaviour of the snails from different locations might lead to differential selection of the morphs for this reason, thus giving spurious evidence for selection on banding. Indeed Wolda himself showed that there are differences in behaviour between snails taken from different colonies (Wolda 1965). Bantock, Bayley & Harvey (1975) found selection against conspicuous (to the human eye) mid-banded morphs in mixed artificial populations of *Cepaea hortensis* and *Cepaea nemoralis*. Although they did not mark the snails, this population was small, isolated and the only one that could be used by the thrushes in the area. Thus the gene frequencies and the source of shell remains at anvils were known accurately. However, the criticism still applies that the established population did not come from within a single homogeneous mixed population, because the *Cepaea nemoralis* were collected from a different locality from the *Cepaea hortensis*. Additionally, Bantock, Bayley and Harvey do not state whether or not the different morphs of *Cepaea hortensis* came from different localities.

Parkin (1971) in a study of predation on *Arianta arbustorum* found a higher frequency of yellow shells amongst predated shells than in the live population in the same woodland area. The converse was found in non-woodland habitats in four out of five areas studied. However, these results could be explained by song thrushes carrying snails from non-woodland sites into woods and vice-versa (Clarke *et al.* 1978).

Some studies have attempted to measure the intensity of the selective forces exerted by song thrushes. However, these estimates may be inaccurate because of the uncertainty of the exact location (and hence gene frequencies) of the population being attacked (Jones, Leith & Rawlings 1977). Selection against yellow morphs of *Cepaea hortensis* was estimated to be approximately 5% in woodland habitats (Cain & Currey 1963) and even stronger on short grass (Cain & Currey 1968). In a study of a sand dune population of *Cepaea nemoralis* a change in background colour over a 34 year period was found to correspond to a decrease in the less cryptic brown morph (Clarke, Diver & Murray 1968). Averaged over the whole period the selection against the less cryptic morphs was estimated to be in the order of 10% (Clarke & Murray 1962).

Although there seems to be a large amount of evidence for predators exerting selection and influencing gene frequencies in terrestrial molluscs, the studies often suffer from methodological problems. Many of them have failed to take into account the pitfalls of sampling (Clarke *et al.* 1978); namely, difficulties in establishing the morph frequencies in the exact localities from which the predators are selecting and ensuring that these hunting areas do not change. The establishment of artificial colonies has been used in some experiments, but, the various morphs have usually been collected from different colonies. Each population may exhibit different behaviour patterns, thus affecting the availability and visibility of the morphs. Behaviour may also differ between morphs within a population (Wolda 1963), therefore even in colonies established from within a panmictic unit the effects of this behaviour cannot be discounted. Possible changes in behaviour of morphs with season, climate or vegetation further complicate the interpretation of many of the studies. It should also be pointed out that in the two papers generally accepted as providing the best evidence of visual selection by thrushes

(Sheppard 1951; Carter 1968a), the sample sizes of prey remains at anvils were very low. Weekly morph percentages were calculated on numbers below one hundred and frequently less than ten. Furthermore, although there was no obvious indication that the available morph frequencies changed during the course of the experiment, this was not explicitly tested.

A criticism of the studies concerned with correlations between morph frequency and background is the anthropocentric judgement of crypsis. The visual world of a song thrush may be very different from that of our own, due to differences in the perception of colour and tone, and differences in the scale and perspective of background components as seen from the position of a hunting thrush.

In summary, research on the pulmonates has produced strong but not conclusive evidence that predators exert selection which acts directly upon genetically determined visible characters.

Evidence for natural selection on visual characters in marine molluscs

Many marine gastropods are polymorphic for shell colour and are subject to selection by a variety of predators. Thus, like some of the terrestrial pulmonates they include predator/prey interactions that can provide useful cases for the study of apostatic selection. Most of the work concerning the effects of predator selection on these polymorphisms has focused on the intertidal *Littorina* and related genera. European littorinid snails are highly variable in colour and morphology, and have undergone many taxonomic revisions (see Raffaelli 1982; Fish & Sharp, 1985 for reviews). Their shell colour polymorphisms are summarised in Table 1.2.

These species are distributed within a vertical zonation on european shores and consequently the importance of the various predators is partially dependent on their respective positions. Shore crabs (*Carcinus maenas*) are the main predators of those littorinids that occur low down on the shore (Pettitt 1975; Heller 1975b, 1976; Raffaelli 1978), although some fish, e.g. the shanny (*Blennius pholis*), may also be important (Quasim 1957; Reimchen

Table 1.2. Some examples of shell colour polymorphism in European species of *Littorina*. Taxanomic status according to Fretter (1980).

SPECIES	DESCRIPTION	SOURCE
L.neritoides (L.)	Grey to black.	Lewis (1964)
L.saxatilis (Olivi)	White to yellow, orange, red, brown, purple, pale violet, greenish grey & black. Bands and tesselations common.	Fretter & Graham (1980)
L.neglecta (Bean)	White to yellow or grey, occasionally brown or red. Usually atleast two dark brown bands. Tesselations common.	Fish & Sharp (1985)
L.nigrolineata (Gray)	White, yellow or reddish brown.	Heller (1975a)
L.arcana (Hannaford-Ellis)	Pale grey, fawn, yellow or brown. Banded and tesselated forms occur.	Hannaford-Ellis (1978)
L.obtusata (L.)	Yellow, olive, brown, black and occasionally orange or red. Commonly reticulated. Occasionally banded.	Smith (1976)
L.mariae (Sacchi & Rastelli)	Yellow, orange, brown, black, rarely olive. Reticulated forms common. Banded forms occasional.	Goodwin & Fish (1977)
L.littorea (L.)	Usually black, rarely red or yellow.	Heller (1975a)

Note. These forms do not necessarily relate to genetically controlled morphs.

1974; Pettitt 1975). The significance of terrestrial predators is less well established, but birds are known to be important predators of many littorinids particularly those occurring high up on the shore (Pettitt 1975; Faller-Fritsch & Emson 1985; Feare & Summers 1985). Of these, the major predators are likely to be the rock pipit (*Anthus spinoletta*) and purple sandpiper (*Calidris maritima*) (Feare & Summers 1985). In fact Gibb (1956) calculated that rock pipits may consume over 14,000 littorinids in one day. Gibb also found that both pipits and turnstones (*Arenaria interpres*) consistently selected small shells. Visual selection as a result of bird predation is therefore most likely to occur on the juveniles.

Littorinid species of the genus *Littoraria* are found in the Indo-Pacific region and predominantly occur on mangrove trees. Although most of these species were previously regarded as *Littorina scabra* (L.), recent taxonomic investigations have established the existence of 20 species, all of which have been transferred to the genus *Littoraria* (Reid 1986). Although all of the species are generally found above the water level on the aerial roots, trunks, branches and foliage of mangroves, as in the European littorinids the species show vertical zonations. The species also vary in their degree of polymorphism and this has been shown to be associated with their respective vertical distributions. The most highly polymorphic species are associated with heterogeneous backgrounds consisting of the tree foliage and branches, whilst the monomorphic uniform brown and darker species occur lower down on the trunk (Cook 1983; Hughes & Jones 1985; Reid 1986).

Little information is available on the degree of predation on *Littoraria* populations, nor the species involved. Predators that have been reported as feeding on *Littoraria* include crabs (Reid 1984), a bird (Lewin's honeyeater (*Meliphaga lewinii*) (Liddy 1984)) and various fish (e.g. toadfish (*Spheroides hamiltoni*), which feed on the submerged juvenile snails (Hughes & Jones 1985; Hughes & Mather 1986).

As in *Cepaea* some of the evidence that these polymorphic snails are subject to visual selection is based upon correlations between morph frequency and background colouration. The first evidence of this in *Littorina* was provided by Pettitt (1973), when he demonstrated that tesselated and banded morphs tend to associate with the habitats on which they are most cryptic (the human eye). Later studies on *Littorina mariae* (Reimchen 1974), *Littorina rudis* (Maton) (now classified as *Littorina saxatalis* (Olivi)) and *Littorina nigrolineata* (Heller 1975b), *Littorina obtusata* (Smith 1976) and *Littorina nigrolineata* (Naylor & Begon 1982) also demonstrated close correlations between morph frequencies and background colour. All these authors attributed the correlations to the actions of predators selecting against conspicuous morphs. Sacchi (1974) and Raffaelli (1979) found correlations between morph frequencies and the degree of exposure to wave action which was not related to the visual properties of the background. They therefore suggested that shell colour is a pleiotropic character which is not subject to direct visual selection. There is similar evidence that non-visual selection on *Nucella* may operate on characters closely linked to shell colour (Berry & Crothers 1974; Sergievskii & Berger 1984).

Crabs and fish (as well as birds) are likely to be significant predators of intertidal prosobranchs. In the British Isles the most ubiquitous species of crab is *Carcinus maenas.* Although the range of colour perception of *Carcinus maenas* is not yet known, some ability to differentiate colours has been found in this species (Buddenbrock & Friedrich 1933) and others (Horridge, 1967; Hyatt 1975; Bursey, 1984). Fish are thought to have a similar range of spectral sensitivity to that of humans (Blaxter 1970). Substantial evidence also suggests that the perceptual abilities of birds is comparable to that of humans (Pumphrey 1948; Suthers 1977; Blough 1979). Therefore, although colour vision is not strictly necessary for selection to occur on colour polymorphisms if the predators use cues based on tone, it is clear that all these predators could contribute to visual selection.

Reimchen (1974) demonstrated visual selection in a fish, the shanny (*Blenius pholis*). In a laboratory experiment he found that the fish preferentially selected yellow morphs when presented on a background of directly illuminated *Fucus*. In this situation dark morphs were cryptic; however, when light was shone through the *Fucus* laminae the yellow morphs became cryptic and were at a selective advantage. Hughes & Jones (1985) showed that in laboratory aquaria toadfish (*Spheroides hamiltoni* and *Spheroides pleurosticus*) would feed on juvenile *Littoraria.* Furthermore, when yellow and brown morphs were presented on dark branches, the fish took an excess of the conspicuous yellow morphs. Visual selection was also suggested to account for the decrease in yellow morphs of *Littoraria* observed after exclusion of predators from mangrove trees (Hughes & Mather 1986). Shorebirds were shown by Giesel (1970) to preferentially select the least cryptic morphs of the limpet *Acmaea digitalis.* Similarly, Schneider (1982) showed that ruddy turnstones (*Arenaria interpres*) feeding on the polymorphic clam *Donax variablis* exerted visual selection against conspicuous morphs. Although Smith (1975) has claimed to have shown visual selection by crabs against conspicuous morphs of *Donax faba* this has been criticised by Schneider (1982).

Colour polymorphisms and the effects of non-visual selection

Of the studies reviewed above, many have provided good evidence of natural selection by predators on polymorphic mollusc populations. However, it is likely that other factors also influence shell morphology and colour morph frequency in these species. Of these factors, one of the most important is likley to be physiological stress through the effect of shell colour on the snails' thermal properties. Light-shelled individuals have been shown to have better heat reflecting properties in *Cepaea* (Emberton & Bradbury 1963; Heath 1975; Garcia 1977), *Littoraria* (Cook & Freeman 1986; Reid 1987) and a species of *Nodilittorina* (Markel (1971). Furthermore, differences in morph colour have been shown to affect activity patterns in *Cepaea* (Jones 1973), micro-habitat partitioning in *Littoraria* (Cook 1986a; Cook & Freeman 1986), salt loss, survival at low salinity and thermostability in *Littorina obtusata* (Sergievskii 1984), metabolic rate (Steigen 1979), reproductive success (Wolda 1967) and survivorship in *Cepaea* (Richardson 1974; Bantock 1974, 1980; Bantock & Ratsey 1980; Tilling 1983).

Interactions between thermal properties and selection for crypsis have been demonstrated in several studies. In a series of investigations (Heller 1981; Heller & Volokita 1981; Heller & Gadot 1984, 1987) it was demonstrated that the desert landsnails

Xeropicta vestalis and *Theba pisana* show banded and cryptic colouration only when shaded by dense perennial vegetation. In the absence of perennial vegetation, the snails are predominantly white-shelled and lack banding patterns, thus affording maximum protection from solar radiation. Furthermore, Heller & Gadot (1984) also showed that the intensity of predation on *Theba pisana* is least in the exposed habitats, due to the lower numbers of the principal snail predator: gerbils (*Gerbillus allenbyi*). Thus, in exposed habitats selective pressure for crypsis is overcome through the combination of thermal stress and lower predation levels.

Cook (1986a) showed that at high temperatures the location of *Littoraria* with respect to the upper (exposed) and lower (shaded) surfaces of leaves was dependent on morph colour. Yellow morphs occurred more often on the upper leaf surfaces whilst dark morphs were predominant on the undersides of leaves. This resulted in a degree of optimal background matching, because in these positions the morphs were most cryptic. Similarly, Sacchi (1966) found that yellow, unpigmented morphs of *Littorina obtusata* occur disproportionally more often on the surface of *Fucus* fronds than darker morphs. Although the causal mechanism was a direct response to bright sunlight, this behavioural adaptation probably reflects the differences between the thermal properties of the colour morphs. Thus, indirectly the yellow morphs tend to distribute themselves disproportionately more often in situations that maximise their degree of crypsis (*sensu* Endler 1978) than expected by chance.

The demonstration of non-visual selection in these species shows that care must be taken in the interpretation of selective predation. Many observations of selection by predators have been proposed as evidence for selection for crypsis (e.g. Sheppard 1951; Wolda 1963; Carter 1968a) however, these results could also occur through interactions between predation and snail behaviour. Disproportionate predation of pale and unbanded snail morphs may arise through excessive predation of active or exposed light-shelled snails during periods of high thermal stress. Therefore, the differing thermal properties of the colour morphs must be taken into account in the design and interpretation of predation studies.

THE MAINTENANCE OF POLYMORPHISMS.

There are several processes that may, at least in theory, maintain polymorphisms; these are discussed below.

Random processes

Proponents of random processes suggest that the polymorphisms are selectively neutral. This view was held by many early workers (see Clarke *et al.* 1978 for review). Lamotte (1951) argued that distributions of some genes in French populations of *Cepaea nemoralis* agreed with theoretical distributions of random drift proposed by Wright (1948). In addition he suggested that selection was unimportant, because of a lack of correlation between morph frequencies and habitat, or between phenotype frequencies of *Cepaea nemoralis* and *Cepaea hortensis* living in mixed colonies. Lamotte also suggested that song thrush predation in France is non-selective because it occurs in winter on buried snails and therefore does not act upon the visual properties of the snails. These conclusions were later strongly criticised by Cain & Sheppard (1954), because the random drift model assumes a high mutation rate for which there is no evidence. Also Lamotte compared the mixed colonies of *Cepaea hortensis* and *Cepaea nemoralis* by recording percentages of yellow shells or unbanded shells. This obscured the effects of selection which are only apparent if the visual properties of the phenotypes are considered.

Since Lamotte´s work many studies have demonstrated that the polymorphism in *Cepaea* is subject to selection strong enough to override the effects of random drift in all but the very smallest populations (Clarke *et al.*, 1978). However, random processes may still be important, especially where predation is uncommon. One such process is that of founder effect. The outcomes of these historical accidents and population ´bottle-necks´ have been demonstrated in a number of studies on *Cepaea* (see Jones, Leith & Rawlings, 1977 for review). This effect is clearly irrelevant to those polymorphic species of *Littorina* and *Littoraria* with planktonic larvae, where substantial gene flow occurs between geographically distinct populations. However, Heller (1975a) showed that the most polymorphic species lacked a planktonic larval dispersal stage, and suggested that this was adaptive because it enabled populations to match their local conditions. But equally, it can be argued that the polymorphism in non-planktonic species is a result of reduced gene flow as a consequence of the reproductive strategy which may have evolved for reasons separate from the polymorphism.

Although random genetic drift and founder principle may influence gene-frequency in some cases, there is no convincing evidence that these processes explain the existence of polymorphisms in most populations of molluscs.

Selection and migration in a heterogeneous environment

In heterogeneous environments gene flow between populations subject to different selection pressures may have the potential to maintain polymorphisms (Levene 1953; Levins & MacArthur 1956). Early models suggested that stable polymorphisms could only be maintained by this process in fine-grained habitats when combined with heterozygote advantage. But later models indicated that morph stability could occur without heterozygote advantage if there is separate population regulation between niches and substantial selection (Maynard Smith 1970) or if there are large numbers of ´patches´ with little spatial correlation between them (Gillespie 1974). However, investigation of these ´spatial heterogeneity´ models indicated that by themselves morph stability is unlikely in most situations (Maynard Smith & Hoekstra 1980), unless there is density dependent habitat selection so that the prey species prefer background patches against which the morphs are most cryptic (Maynard Smith 1970; Maynard Smith & Hoekstra 1980; Cook 1986b), or if the prey species masquerade as particular background elements, such that the ability of predators to distinguish prey from the background is frequency-dependent (Cook 1986a). Habitat selection which maximises the level of crypsis has been shown to occur in *Littoraria* (Cook 1986a), although the mechanism leading to optimal habitat selection for crypsis was the thermal properties of the snails, not direct behavioural responses to the background colour. Similar thermal properties in *Cepaea* and *Littorina* may also indirectly contribute to optimal habitat selection for crypsis, although no data exist at present to support this. Cases of polymorphic prey masquerading as specific background elements has been suggested for *Littoraria pallescans* on a background of mangrove (*Rhizophora*) foliage (Cook 1983) and *Littorina obtusata* amongst the bladders of *Fucus* (Smith 1976).

Stable polymorphisms through spatial heterogeneity may also occur when combined with apostatic selection (Endler 1978; Cook 1986b). However, in situations where prey are selected by more than one kind of predator, variations in predator vision, foraging decisions, learning and temporal changes in background combined with variation in the timing of selection can cause transitions from predictions of polymorphism to monomorphism (Endler 1988).

Although spatial heterogeneity combined with selective predation has been proposed as a mechanism maintaining polymorphisms in *Littorina obtusata* (Smith 1976) and *Littorina maraie* (Reimchen 1979), to date there is no quantitative information on the magnitude of this effect in molluscs. However, there is little doubt that this process must play some part in the maintenance of genetic diversity (Clarke *et al.* 1978)

Heterozygous advantage.

Heterozygote advantage has been proposed as a means of maintaining the polymorphism in *Cepaea* (Cain & Sheppard 1954; Ford 1971). However, there is no evidence that this process acts on *Cepaea* (because there is no reliable method for detecting the heterozygotes), and only one study has succeeded in demonstrating it in other molluscs. Komai & Emura (1955) found faster growth rate in double heterozygotes for colour and banding, in the landsnail *Bradybaena similaris*. Therefore, heterozygote advantage as a process maintaining polymorphisms remains generally unsubstantiated.

Frequency dependent mating.

Frequency dependent sexual selection occurs whenever a departure from random mating is a function of the frequencies of the genotypes involved (Ayala & Campbell, 1974). This could maintain polymorphisms if rare morphs are more likely to be chosen and mated with than other morphs. However, extensive sampling of wild copulating pairs of *Cepaea nemoralis* by Lamotte (1951) found no evidence of non-random mating in this species. Similarly Sergieskii (1983) found that shell colour did not influence the choice of mates in *Littorina obtusata* (although there was positive assortative mating for shell size). Thus, it is unlikely that frequency dependent mating maintains polymorphisms, at least in those species studied. A more likely mechanism is frequency-dependent selection by predators.

APOSTATIC SELECTION

Clarke (1962) suggested the term "apostatic selection" to describe when predators kill a disproportionately high number of common forms of prey, thereby confering a selective advantage on visually distinct rare forms (apostates). This theory that predators could directly maintain colour polymorphisms was based upon earlier ideas of frequency-dependent selection by Poulton (1884), Fisher (1930) and Cain & Sheppard (1954). However, Clarke expanded their ideas and provided evidence for apostatic selection in a reanalysis of experiments carried out by Popham (1941, 1942) on predation of the corixid bug (*Sigara distincta*) by rudd (*Scardinius eryopthalmus*). His results showed that the visually distinct phenotypes were preyed on more often than expected at high frequencies and less than expected when rare. Clarke also presented comparable evidence from the work of Tinbergen (1960), on the predation of insects by birds.

Allen & Clarke (1968) presented further evidence of apostatic selection by birds and developed a technique for demonstrating this. They presented wild passerine birds with dimorphic artificial prey made from pastry dough dyed with food colouring. Trials were carried out in which the birds were either presented with prey in equal numbers after conditioning on one type, or prey were presented together, with one type nine times as common as the other. Using the first method Allen & Clarke showed that birds preferentially selected the prey type that they had been ´trained´ on. Similar results were obtained from subsequent studies with artificial baits, natural and semi-natural prey (Table 1.3). However, this type of presentation is not such a close match to natural polymorphic situations as the latter, where the two prey are presented simultaneously. Allen & Clarke´s

Table 1.3. Investigations of apostatic selection on artificial, semi-natural and real polymorphic prey: training experiments. (Table adapted from Allen (1988)).

The number of prey refers to the number of 'morphs' in the 'population'. TB = training bias.

REFERENCE	PREDATOR	PREY	RESULT	NOTES
		(a) Prey artificial		
Allen & Clarke (1968) & Allen (1974)	birds	baits (2: green, brown)	TB	
Allen (1973)	birds	baits (9: various hues of green and brown in a quasi-continuous distribution)	TB	1
Allen (1984)	birds	baits (2: from various hues of green & brown)	TB	
Croze (1970)	crows	mussels over meat (2:various combinations of shapes and colours)	TB	2
Oates (in Cook 1971)	birds	baits (red,yellow)	TB	
Raymond (1984, 1987)	birds	flat baits (2: striped, plain)	TB	
Shelton (1986)	birds	baits (2: discoid, cylinders)	TB	3
Soane & Clarke (1973)	lab mice	baits (2: peppermint, vanilla)	TB	4
		(b) prey natural or semi-natural intraspecific variants		
Allen *et al.* (1988)	birds	*Cepaea hortensis* (2: Y0,Y5)	TB	5
Clarke (1961)	song-thrushes	*Cepaea hortensis* (2: Y0,Y5)	NO TB	
den Boer (1971)	coal tit	moth larvae (*Bupalus piniarius*)(2: green, yellow)	TB?	6
Harvey *et al.* (1975)	song-thrushes	*Cepaea nemoralis* & *Cepaea nemoralis* (2: Y0, B0)	TB	7

NOTES

(1) Training on modal colour resulted in increased variance of prey population.
(2) Prey cryptic; training bias unaffected by degree of similarity of prey.

(3) Training bias caused by visual preference or familiarity with handling technique?
(4) Training bias for familiar scent.
(5) Shells filled with pastry.
(6) Only one bird; green prey cryptic, yellow conspicuous; trained on green only.
(7) Shells filled with breadcrumbs; training bias for colour stronger the training bias for size.

Scientific names of species referred to in the table.

Crow (*Corvus corone*).
Song thrush (*Turdus philomelos*).
Coal tit (*Parus ater*).

results from these '9:1' experiments showed that the birds preferred the commoner prey type. Since then many similar 'multi-frequency' experiments have been undertaken using artificial baits, natural and semi-natural prey and a range of predators (Table 1.4). Most of these have all shown that in controlled conditions visually hunting predators can feed in a frequency dependent manner. Among these experiments specific studies have also demonstrated that the magnitude of the response is affected by prey density (Cook & Miller 1977), palatability (Greenwood, Wood & Batchelor 1981) and degree of crypsis (Cooper 1984). Furthermore the direction of selection may be reversed at very high prey densities thus leading to anti-apostatic selection.

Clearly there is good experimental evidence for apostatic selection as a general phenomenon in visually hunting predators. Furthermore, mathematical investigations have suggested that this form of frequency-dependent selection could theoretically maintain polymorphisms, even in the face of frequency-independent selection (Haldane & Jayakar 1963; Clarke & O'Donald 1964; Cook 1965; Endler 1988). However, the evidence that apostatic selection acts upon naturally occurring polymorphic prey is very scarce indeed.

The evidence for apostatic selection on *Cepaea* is based on comparisons of frequencies of shell phenotypes in mixed colonies of *Cepaea nemoralis* and *Cepaea hortensis*. Clarke (1962a,b) showed that morph frequencies are negatively associated in the two species. Clarke argues that this is indirect evidence of apostatic selection, because it is expected that selection acting on common morphs in one species will also select against any similar morph in the other, if they share a common predator. In such a situation it will be advantageous for individuals of either species if their visual appearance is distinct from the most common morph of the other species, if predation is frequency-dependent. Therefore, apostatic selection is expected to cause a divergence in visual appearance between species in mixed polymorphic populations subject to predation.

Clarke's data were criticised because they were biased by including populations in which morph frequencies were not affected by visual selection (Carter 1967; Cook 1965). Carter also argued

Table 1.4. Investigations of apostatic selection on artificial, semi-natural and real polymorphic prey: multi-frequency experiments. (Table adapted from Allen (1988)).

The number of prey refers to the number of ´morphs´ in the ´population´. AS = apostatic selection; PAS = potential apostatic selection; FDS = frequency-dependent selection.

REFERENCE	PREDATOR	PREY	RESULT	NOTES
		(a) Prey artificial		
Allen & Clarke (1968) & Allen (1972,1976)	birds	baits (2: green, brown)	PAS	1
Bond (1983)	domestic pigeons	´seeds´ (2: beans, wheat)	AS	2
Cook & Miller (1977)	Japanese quail	baits (2: blue, red)	AS	3
Cooper (1984)	birds	baits (2: orange, grey)	AS	2
Fullick & Greenwood (1979)	domestic chicks	crumbs (2: green, brown)	AS	
Gendron (1982)	bobwhite quail	baits (2: green, brown)	AS	4
Greenwood *et al.* (1981)	birds	baits (2: yellow, red)	NO FDS	5
Greenwood *et al.* (1981)	domestic	chick crumbs (2: green, brown)	AS	6
Harvey *et al.* (1974)	birds	baits (2: green, brown)	AS	
Horsley (1978)	birds	baits (2: yellow, brown)	NO FDS	
Manly *et al.* (1972)	Japanese quail	baits (2: blue, red)	AS	
Shelton (1986)	birds	baits (2: discoid, cylinders)	AS	
Shelton (1986)	birds	baits (11: various shapes, in quasi-continuous distribution)	AS	7
Tucker & Allen (1988)	humans	computer-generated images (2: T-shape, circle)	AS	4
Weale *et al.* (1988)	humans	computer-generated images (4: different shapes)	AS	8

Willis *et al.* (1980)	domestic chicks	crumbs (2: red, green; green, yellow; red, yellow)	NO FDS	
Willis *et al.* (1980)	domestic	crumbs (2: green, brown)	AS	9

(b) prey natural or semi-natural intraspecific variants

R. W. Arnold (unpublished)	song-thrushes	*Cepaea nemoralis* (2: PO, YO ;BO, YO)	AS?	10
Maskell *et al.* (1977)	stickle-backs	*Asellus aquaticus* (2: light, dark)	AS	
Popham (1941, 1942)	Rudd	*Sigara distincta* (3: shades of brown)	AS	11
Reid (1987)	unknown	*Littoraria filosa* (2: yellow, brown)	AS	12

NOTES

(1) Apostatic selection unaffected by background.
(2) Apostatic selection stronger when prey inconspicuous.
(3) Apostatic selection increased with density.
(4) Apostatic selection when prey inconspicuous; no apostatic selection when prey conspicuous.
(5) Both morphs unpalatable
(6) Apostatic selection weaker when both prey unpalatable than when both palatable.
(7) Selection against modal colour increased variance of prey population.
(8) Apostatic selection by adults, not by children.
(9) Irregular Apostatic selection. No effect of density.
(10) Artificial colonies of live *Cepaea*.
(12) Reanalysed by Clarke (1962a).
(11) Manipulation of morph frequencies on mangroves.

Scientific names of species referred to in the table.

Domestic pigeons (*Columba livia*).
Japanese quail (*Coturnix coturnix*).
Bobwhite quail (*Coturnix virginianus*).
Song thrush (*Turdus philomelos*).
Sticklebacks (*Gasterosteus aculeatus*).
Rudd (*Scardinius erythrophthalamus*).

that if Clarke´s observations were evidence for apostatic selection, then it should be possible to show that morph frequencies are more dissimilar in mixed colonies, than in pairs of adjacent unmixed colonies. However, Carter found the reverse. In a reply to Carter, Clarke (1969) presented more evidence for the negative correlation between morphs, and argued that comparisons on close unmixed colonies is not a valid test, because differences in habitat (and therefore background) between the colonies, could obscure the effects of the observations they were designed to detect. Therefore considering these complications, the significance of these results as indirect evidence for apostatic selection remains unclear. Furthermore, subsequent studies of mixed colonies of *Cepaea* failed to find similar divergences in morph frequency (Bantock & Noble 1973; Bantock & Harvey 1975; Arthur 1978, 1980).

Evidence that song thrushes and other passerines can select prey in an apostatic manner with respect to visible characters, was presented by Harvey, Birley & Blackstock (1975) and Allen, Raymond & Geburtig (1988) in experiments using bread-stuffed *Cepaea* shells (see Table 1.4). They found that after ´training´ on a particular morph the birds selected the familiar shells more often than expected from a polymorphic population. However, the ´training´ method may not be directly relevant to natural polymorphic situations (Greenwood 1985). Bantock, Bayley & Harvey (1975) did an experiment with wild song thrushes feeding on mixed but artificial populations of *Cepaea hortensis* and *Cepaea nemoralis*. They found that the thrushes apparently produced an equilibrium of frequencies, which they suggested was the result of directional selection modifying each population of morphs, until the final frequencies were maintained by a balance between conspicuousness and apostatic selection. However, this evidence is flawed because it does not rule out the simpler hypothesis that the stabilisation of the frequencies is due to the birds becoming acquainted with the rare morphs later in the experiment. Apostatic selection is not demonstrated, because there is no evidence for a long term advantage for the rare morph. As they state themselves, to show apostatic selection conclusively it is necessary to present a wide range of morph frequencies.

Summarizing the case for apostatic selection as a process maintaining the polymorphism in *Cepaea*, we see that: 1) there is good evidence that visual hunting predators (including the song thrush) feed on artificial prey in an apostatic manner, 2) there is some indirect evidence that the morph frequencies in mixed populations are influenced by apostatic selection, 3) to date, there is no direct evidence of apostatic selection on natural or artificial populations of *Cepaea*.

Apostatic selection has also been suggested as a process maintaining the polymorphisms in the clam, *Donax variablis* (Moment 1962), African land snail *Limicolaria martensiana* (Owen 1963) and various species of *Littorina* (Reimchen 1974; Smith 1976; Faller-Fritsch & Emmerson 1985) and *Littoraria* (Hughes & Mather 1986). However, there is no direct evidence to support any of these cases, except for *Littoraria*, through a study by Reid (1987).

Reid carried out a large scale and detailed field experiment in which he manipulated the morph frequencies of sub-populations of *Littoraria filosa* on isolated mangrove trees. The results showed that ´survival´ (measured as those remaining after five succesive periods of 2 weeks) of the yellow and dark morphs was frequency dependent, such that the rare morphs were at a selective advantage. Although, the study did not establish the selective agent involved, it was assumed to be due to selective visual predation. Previous studies have suggested that visual selection occurs (Hughes & Jones 1985; Hughes & Mather 1986) and the predators may include crabs (Reid 1984), birds (Liddy 1984) and various fish (Hughes & Mather 1986). To date, this experiment, combined with the previous studies, provides the only evidence for apostatic selection contributing towards the maintenance of a polymorphism in a natural population of prey.

For a detailed review of apostatic selection see Allen (1988).

FREQUENCY-DEPENDENT PREDATION

Although population geneticists have been interested in positive frequency-dependent selection because of its potential role in the maintenance of polymorphisms, ecologists have also investigated this process with respect to its possible influence in stabilizing prey populations and maintaining species diversity (Murdoch 1969, 1973; Murdoch & Oaten 1975; Roughgarden & Feldman 1975; May 1977; Hassel 1978). Population geneticists have termed the process "apostatic selection" (Clarke 1962), whilst ecologists refer to the same phenomena as "switching" (Murdoch 1969). From a behavioural point of view the terms are synonymous, because they both refer to frequency dependent-selection by predators, (i.e. frequency-dependent predation) although the first acts upon morphs of species and the second acts on separate species. Therefore the selective effects of each process are obviously different; apostatic selection may maintain intra-specific diversity, switching may maintain inter-specific diversity. Clearly frequency-dependent predation may be an important process creating and maintaining diversity in nature.

MECHANISMS OF FREQUENCY-DEPENDENT PREDATION

There are many mechanisms which can be expected to produce frequency dependent predation. In fact, Greenwood (1984) states that "there are so many circumstances in which one expects to find it that one would not be surprised to discover that frequency-independent selection is the exception rather than the rule". These mechanisms explicitly assume that predators maximise their fitness by responding to perceived changes in relative and absolute prey density. They can be divided into categories relating to the four basic components of predatory behaviour: prey encounter rate, detection of an encountered prey, probability of attacking a detected prey and probability of successful capture of an attacked prey (Holling 1966).

Prey encounter rate

Patch use

Predators may learn to recognise good hunting areas and then preferentially allocate hunting time to these more ´profitable´ (i.e. highest net reward per unit handling time) food patches (Royama 1970; Murdoch *et al.* 1975; McNair 1980; Bayliss 1982). Therefore prey types inhabiting profitable patches will be subject to increased attention by predators. This process may act on a large scale, between habitats, e.g. a song thrush may restrict feeding to a pasture were prey are most abundant and will therefore encounter more earthworms than snails, the latter being restricted to hedgerows. Alternatively micro-habitat partitioning may result in frequency-dependent predation. For instance two caterpillars may be regularly encountered by a predator, but the commonest is exclusively found on the upper surface of the leaves, whilst the rarer is found on the underside. In this situation a predator may maximize its encounter rate if it only searches on the upper leaf surfaces.

Prey may also be temporally separated. In these circumstances it may benefit a predator to hunt preferentially during the active period of the commoner prey, if its hunting time is limited by other factors (e.g. courtship requirements, nest building, thermo-regulation, etc.).

Prey detection

Search image

Tinbergen (1960) found switching behaviour by tits (*Paridae*) feeding on insects in the wild. Tinbergen suggested that this was due to the tits learning to see the cryptic prey through a change in perception. This process he termed the development of a "specific search image", and suggested that it incorporates "a highly selective sieving operation on the visual stimuli reaching the retina". Current pyschological theory suggests that some form of selective attention (see Johnston & Dark 1986 for review) is likely to be involved (Croze 1970; Krebs 1973; Bond 1983). The behaviour may produce frequency-dependent predation because it is likely that search images are not developed for infrequently encountered prey. Thus, the search image is a process that effectively increases the detection rate of common cryptic prey. Some workers suggest that search image development is likely to be density dependent because at high densities all prey types will be encountered sufficiently often for search images to be developed for all types, whereas at low densities search images may not be formed for any prey (Tinbergen 1960; Holling 1963; Krebs 1973). However, as yet, there is no evidence to support this hypothesis of an interaction between prey density and search image. Also, it may be argued that mixed processing is always costly, irrespective of the prey density (Greenwood 1984).

Although Tinbergen (1960) developed the search image concept, his study did not present any direct evidence for it (Royama 1970). In fact many of the mechanisms discussed in this section may account for Tinbergen´s observations.

Direct evidence of the development of a search image by predators was claimed to have been provided by Dawkins (1971a, b) in experiments using domestic chicks (*Gallus* sp.) searching for dyed rice grains on a range of coloured backgrounds. Dawkins observed that a delay occurred before the chicks took the cryptic rice grains, and suggested that the behavioural change was due to the chicks learning to see the cryptic grains. Later studies by Pietrewicz & Kamil (1979) using blue jays (*Cyanocitta cristata*) trained to select projected images of Noctuid moths, Lawrence (1985a, b) with blackbirds (*Turdus merula*) and Gendron (1986) using quail (*Cortnix courtnix*) also claimed to have demonstrated search image development in these predators. Additionally the studies of de Ruiter (1952), Croze (1970), Den Boer (1971) and Murton (1971) attribute their observations to search image development; however, in these studies, alternative explanations cannot be ruled out. These studies (Dawkins 1971a,b; Pietewicz & Kamil 1979; Lawrence 1985a,b; Gendron 1987) had been widely accepted as providing strong and direct experimental evidence for search image development, until Guilford & Dawkins (1987) suggested an alternative explanation.

Guilford & Dawkins pointed out that although the experiments conclusively demonstrated an increase in the ability of the predators to detect cryptic prey, this could have been caused by the predators learning to decrease their search rate when searching for cryptic prey, thereby increasing their probability of detecting prey. This ´search rate hypothesis´ was based upon the search rate optimization model of Gendron & Staddon (1983,1984) which explicitly investigated the efficiency of foraging with respect to the trade off between the rate of search and the probability of detecting cryptic prey, and its effect on overall prey capture rate.

Comparison of the search image and search rate hypotheses led Guilford & Dawkins to propose two predictions of the search rate hypothesis that could be used to distinguish between them in experimental studies. First, increased ability to detect cryptic prey will be caused by a decrease in search rate, but the search image hypothesis makes no such prediction. Second, perceptual changes associated with search image development should interfere with the ability to detect other equally cryptic prey, whereas the search rate hypothesis predicts that the decrease in search rate should enhance the ability to detect other equally cryptic prey. The previous studies discussed above were re-examined by Guilford & Dawkins (1987) in relation to these predictions and were shown to be flawed because on the available data they failed to distinguish between the two hypotheses.

Guilford & Dawkins (1987) also suggested that apostatic selection would not occur as a result of modifications in search rate. However, this is not strictly true, because the model of Gendron & Staddon (1983) predicts that predation on the conspicuous morph will be potentially frequency-dependent (Greenwood 1984), and see below.

The predictions of Guilford & Dawkins remain to be tested in any artificial or natural predator-prey system. Thus, at present there is no direct evidence that predators form search images, and consequently no evidence that search image development can directly produce frequency-dependent predation.

Despite frequent discussion and warnings (Dawkins 1971a; Krebs 1973, Murdoch & Oaten 1975) the term "search image" has often been misinterpreted and misused (see Lawrence & Allen 1983 for review). In many cases studies demonstrating frequency-dependent predation (e.g. by Bantock, Bayley & Harvey 1974; Harvey, Birley & Blackstock 1975; Cornell 1976; Gendron 1982 (cited in Lawrence 1984); Bond 1983) attributed their results to be evidence for search image devlopment, through interpretation of the term in a very wide sense. This is a misuse of the term, as stated by Murdoch & Oaten (1975) "the search image hypothesis is not equivalent to switching or apostatic selection".

Recognition of unfamiliar prey

Unfamiliar food sources may not be recognised as food and thereby cause frequency-dependent predation (Murdoch 1969; Cornell & Pimentell 1978; Bergelson 1985), if predators encounter rare prey so infrequently that they never learn that it is edible. Also, alternative prey may become available whilst predators are concentrating on other familiar food sources, and thus the novel prey may be temporarily overlooked. These mechanisms lead to permanent and temporary frequency-dependent predation respectively. The observations by Tinbergen (1960) can possibly be explained by the latter. Avoidance of unfamiliar prey have been demonstrated in several studies (e.g. Coppinger 1969, 1970; Partridge 1981).

The process of learning to recognise a novel prey as a food resource has been confused with the development of a search image (Pietrewicz & Kamil 1981). Although they are similar in that they affect prey detection rate, the recognition of novel prey does not incorporate a change in perception by the predator, merely the establishment of the association between certain visual stimuli and a potential food resource.

Search rate optimization

Gendron & Staddon (1983,1984) and Gendron (1986) showed that a predator can maximize its prey detection rate by optimizing its search speed, and that the optimal travel speed is greater for a conspicuous and abundant prey. Therefore if a predator is searching for prey types that differ in conspicuousness, and the most conspicuous type is common, then the optimum search speed will be faster than the optimum for the rare type. Thus, although the predator will always take an excess of the most conspicuous type, more will be taken when common than rare, i.e. predation will be frequency-dependent.

Probability of attacking a detected prey

Positive frequency-dependent predation can be expected in situations where prey are Batesian mimics or masqueraders (see Greenwood 1984 for review). However, these cases will not be discussed in detail here, because this thesis is only concerned with predation on non-mimictic prey.

Optimal diet selection

In theory frequency-dependent predation may occur if two prey types differ in the benefits they provide (Hubbard *et al.* 1982; Stephens & Krebs 1986), because a predator may maximize its fitness by restricting selection to the most beneficial prey type if its density rises above a certain threshold level. Although this model predicts switching, it is the absolute density of the most beneficial prey and not the relative frequency of the prey types that dictates the predicted diet. The value of the threshold level is dependent on relative profitabilities, densities, rate of search and handling times for the two prey.

Minimization of sampling costs

The previous mechanism depended on predators being able to rank prey according to profitability. This may be achieved through inherited responses to stimuli, application of simple ´rules of thumb´ (e.g. ´biggest is best´) or by sampling. If predators need to sample prey to assess their profitability, then this is a constraint upon the optimization of foraging through additional time and effort. However, this cost may be minimized by restricting sampling to common prey types, as these are potentially the most useful food resources (Greenwood 1984). If these turn out to be profitable the predator may ignore the less abundant prey types. Positive frequency-dependent predation may therefore occur, especially at high prey densities, when there is little need to sample novel food when familiar food is abundant.

Probability of successful capture of an attacked prey

Effects of experience

Greater success in capturing and efficiently handling prey through experience (e.g. Partridge & Green 1987) is likely to create frequency-dependent predation (Lawton, Beddington and Bonser 1974; Bergelson 1985). This mechanism may act directly through unsuccessful captures of rarely encountered prey, as a result of unfamiliar antipredator tactics. Additionally, experience may reduce handling time, thereby increasing the profitabilities of common prey. In this situation positive frequency-dependent predation may occur as a result of prey becoming more profitable when common.

Reduction of mixed processing costs

Learning to catch, manipulate, prepare and ingest food may require considerable time and effort. Additionally these skills may be quickly forgotten if they are not regularily reinforced. In these circumstances there may be considerable costs in maintaining a diverse diet (Greenwood 1984). Therefore a predator may benefit by restricting the development of specialised processing to common prey.

Mechanisms not dependent on optimization theory

Positive frequency-dependent predation may be the result of an innate response, in which common forms are preferred simply because they are common. This hypothesis has no clear demonstrable advantage to the predator, and therefore is not based upon a maximization of fitness model. However, it is probably the simplest explanation of frequency-dependent predation, and has yet to be disproved.

The importance of the various mechanisms discussed above will vary with circumstances, and not all of these are relevant to apostatic selection on polymorphic prey. Mechanisms relating to prey profitability and large scale habitat differences are unlikley to occur in most polymorphic situations.

The mechanisms discussed have been developed mainly on theoretical grounds (with the exception of search image development), and have very little supporting evidence. As yet there have been no studies demonstrating any of these mechanisms as causal processess for frequency-dependent predation in laboratory experiments or in nature.

MODELS OF APOSTATIC SELECTION AND ANALYTICAL METHODS

Descriptive models and the analysis used to evaluate the effect of frequency on selection in predation experiments has been the subject of much discussion (Cook 1965; Elton & Greenwood 1970; Manly 1973, 1974, 1978, 1980; Manly *et al.* 1972; Chesson 1978; Cock 1978; Horsley 1978; Greenwood & Elton 1979; Elton & Greenwood 1987; Gendron 1987).

The two most commonly used models for the analysis of experiments on frequency-dependent selection by predators are the Elton & Greenwood (1970) and Manly (1973) models.

The Elton & Greenwood (1970) model

This model takes the form:

$$e_1/e_2 = (VA_1/\ A_2)^b \qquad b > 1$$

Where: e_1 and e_2 are the totals of the two prey types eaten,
A_1 and A_2 are the totals of the two prey types available,
V is the measure of frequency-independent selection,
b is the measure of frequency-dependent selection.

In this model values of $V = 1$ and $b = 1$ correspond to no selection. In experiments where a range of prey frequencies are presented to the predators and corresponding e_1/e_2 values obtained, the parameters b and V can be estimated by either log-log regression or log-linear least squares methods. Although the model can be easily generalized to more than two forms of prey (Greenwood & Elton 1979), only one describing the overall frequency-dependent component is produced.

The Manly (1973) model

Manly's linear model takes the form:

$$B_1 = \log_{10}(r_1/A_1) \;/\; (\log_{10}(r_1/A_1) + \log_{10}(r_2/A_2))$$

Where: B_1 is the probability that the next morph selected will be type 1, and is thus a measure of relative risk of predation,
r_1 and r_2 are the totals of the two prey types remaining at the end of each predation trial,
A_1 and A_2 are the totals of the two prey types available at the beginning of each trial.

The B values (referred to as Manly's Beta selection coeffcients) can be transformed by arcsine transformation to allow parametric analysis. These transformed values range from zero to 90, and where only two prey types are involved, the absence of selection is indicated by a Beta value of 45.

The effect of morph frequency on Beta can be investigated by linear regression analysis, assuming the relationship:

$$B_1 = a + cA_1 \;/\; (A_1 + A_2)$$

Manly's model can also be generalized to many prey types. This generates frequency-dependence estimates for each morph, thereby allowing the assessment of the response of different morphs to changes in frequency, and the influence of other morph frequencies on selection. Thus it is useful for analysing single sets of data for complex interactions between morph frequencies and selection. However, the number of parameters generated makes comparisons of overall frequency-dependence difficult, and for this the Elton & Greenwood model is more useful.

In contrast to Elton & Greenwood's model the Manly model takes account of prey depletion in experiments where eaten prey are not replaced. However, Elton & Greenwood criticised this approach on the *a priori* grounds that it is unrealistic to assume that the predator does not change its behaviour through the trial if the prey proportions change. Although Elton & Greenwood's analytical method can also be used for trials where eaten prey were not replaced, the frequency-dependent selection component will be underestimated. Manly also criticized the Elton & Greenwood model for lacking any underlying theoretical basis concerning predator behaviour. Manly´s model was explicitly based upon the changes in relative risk assumed to occur as a result of changes in relative prey density. However, emprical tests of the models have shown that both provide good fits to available data for experiemnts with two prey types (Greenwood & Elton 1979; Gendron 1987), although the Greenwood & Elton model provided a better fit, particularly at extreme prey frequencies.

AIMS OF THE STUDY

This review of current knowledge on visual predation of polymorphic prey, apostatic selection and its causal mechanism has identified numerous areas where information is lacking. In some cases the theoretical models are poorly developed (e.g. the psychological and behavioural basis of predator searching strategies and our understanding of selective interactions in multimorphic prey populations), but in most cases it is empirical evidence that is needed to test developed theories. Therefore, this study attempted to gain information in some of these under-researched areas through observational and where appropriate experimental studies.

In particular the original aims of this research study were:

(1) To study a predator-polymorphic prey system and establish whether predators exert visual selection on these prey and which factors affect the degree and direction of selection.

(2) To establish whether predators could exert apostatic selection on natural polymorphic prey, by laboratory and large scale field experiments.

(3) To establish the behavioural mechanism underlying apostatic selection in visually hunting predators.

CHAPTER 2

SONG THRUSH PREDATION ON *CEPAEA HORTENSIS* AND OTHER LANDSNAILS

INTRODUCTION

Although many landsnails are polymorphic for shell colour, body colour and banding patterns, most of the studies on selection on these characters have concentrated on the two sibling species *Cepaea nemoralis* and *Cepaea hortensis* and their major predator, the song thrush (*Turdus philomelos*). Indirect evidence suggests that thrushes and other visually hunting predators are the selective agents causing correlations between morph frequency and habitat type in *Cepaea nemoralis* (Cain & Sheppard 1950, 1952, 1954; Currey, Arnold & Carter 1964; Cameron 1969b; Greenwood 1974) and *Cepaea hortensis* (Clarke 1960; Carter 1968b; Cameron 1969a; Greenwood 1974). Colonies of *Cepaea nemoralis* in habitats with dark backgrounds, such as beechwoods, contain high proportions of brown and pink unbanded shells, whilst hedgerows and rough grassland have higher frequencies of yellow and banded morphs, apparently matching the lighter and variegated appearance of the background. Similarly, *Cepaea hortensis* morphs are generally dark and uniform in woodlands and lighter and more frequently banded in grass and hedgerow habitats. However, in *Cepaea hortensis* cryptic dark and uniform morphs are five-banded shells with fused bands.

Comparisons of the remains of *Cepaea* shells at thrush anvils with the morph frequencies of the local live populations provide further evidence for selection for crypsis in the two species (Sheppard 1951; Cain and Sheppard 1954; Goodhart 1956; Sacchi 1956; Wolda 1963; Arnold 1966; Carter 1968a; Cain and Currey 1968) and *Arianta arbustorum* (Parkin 1971). Clarke *et al.* (1972) have criticised some of these studies because the location (and hence the morph frequencies) of the population on which the thrushes had been feeding could not be reliably established. Furthermore, the changes in selection noted in some of these studies (Goodhart 1956; Cameron 1969a) might have been due to changes in the area hunted by the song thrushes. However, the studies by Sheppard (1951); Wolda (1963). Arnold (1966); Carter (1968a) and Cain & Currey (1968) used marked snails and thereby escaped this problem. Yellow morphs have been shown to be preferentially selected in woodland populations (Sheppard 1951), and although their selective disadvantage decreased from April to May, this trend reversed later in the season (Wolda 1963; Carter 1968a). These fluctuations in selective value are usually thought to be related to seasonal variation in background colour caused by the different growth stages of the vegetation. Such fluctuations in selection were not found in beechwoods, where the background is consistently dark; yellow morphs were always at a selective disadvantage (Arnold 1966).

The studies of Sheppard (1951); Carter (1968a) and Cain & Currey (1968) found no evidence for differential selection on banding in *Cepaea*. Although Lamotte (1950) and Cain & Sheppard (1954) claimed to demonstrate selection on the banding polymorphism, the studies suffered the same flaw mentioned above: the morph frequencies of the live snail population could not be reliably established. Wolda (1963) and Bantock (1971) used marked snails to overcome this problem and found selection for banding. However, they used experimental colonies with the different morphs orginating from separate populations. Clarke *et al.* (1978) point out that both results could have been due to differences in behaviour between snails from different localities.

The studies discussed above have led to the generally accepted view that song thrush predation results in selection on some components of the visual polymorphism of *Cepaea* (Jones, Leith & Rawlings 1977; Clarke *et al.* 1978; Cain 1983). Furthermore, the demonstration of selection has formed the basis for the suggestion that song thrush predation itself might be a factor that contributes to the maintenance of the polymorphism through the process of apostatic selection (Clarke 1962a). Although a wealth of experimental evidence indicates that predators can behave in an apostatic manner (see Allen 1988 for review), and that this process can potentially maintain polymorphisms (Haldane & Jayakar 1963; Clarke & O'Donald 1964; Cook 1965), to date apostatic selection remains to be demonstrated as a process affecting natural populations of *Cepaea*.

In order to investigate the processes of selection by song thrushes and ultimately to test directly the apostatic selection hypothesis the following study was carried out at Rogate, Sussex.

The aims of the study were:

(1) To gain background information on the periodicity of snail predation by thrushes and the factors that affect it´s intensity.

(2) To investigate interspecific selection of landsnails by song thrushes and intraspecific selection on *Cepaea hortensis* morphs, by comparing snail remains at anvils between predation periods and with the available live snail population.

(3) To establish the *Cepaea hortensis* morph frequencies, the population size, and the proportion of the population predated.

It was originally intended that these data would be used to establish the feasability of a large scale manipulative experiment in which the morph frequencies would be altered, in order to test for apostatic selection.

STUDY AREA

The study was carried out at Rogate Field Station, Rogate, West Sussex. This is land owned by the University of London and is used as a field station by Kings College. Rogate is a small village approximately 60 metres above sea level and located in the Rother Valley, 5 km north of the South Downs. The surrounding area is primarily agricultural with cereals the predominant crops, although there are some areas of mixed farming. The Field Station includes a garden and three fields with rough grass, patches of bramble (*Rubus* sp.), stinging nettle (*Urtica dioica*) and some sapling trees (mainly birch (*Betula* sp.)). The site is surrounded by tall unmanaged hedgerows and stands of mature deciduous trees (predominantly oak (*Quercus robur*) and horse chestnut (*Aesculus hippocastanum*)). The distribution of the main habitat types and site topography are shown in Figures 2.1 and 2.2. Plates 2.1 - 2.4 give views of the study site.

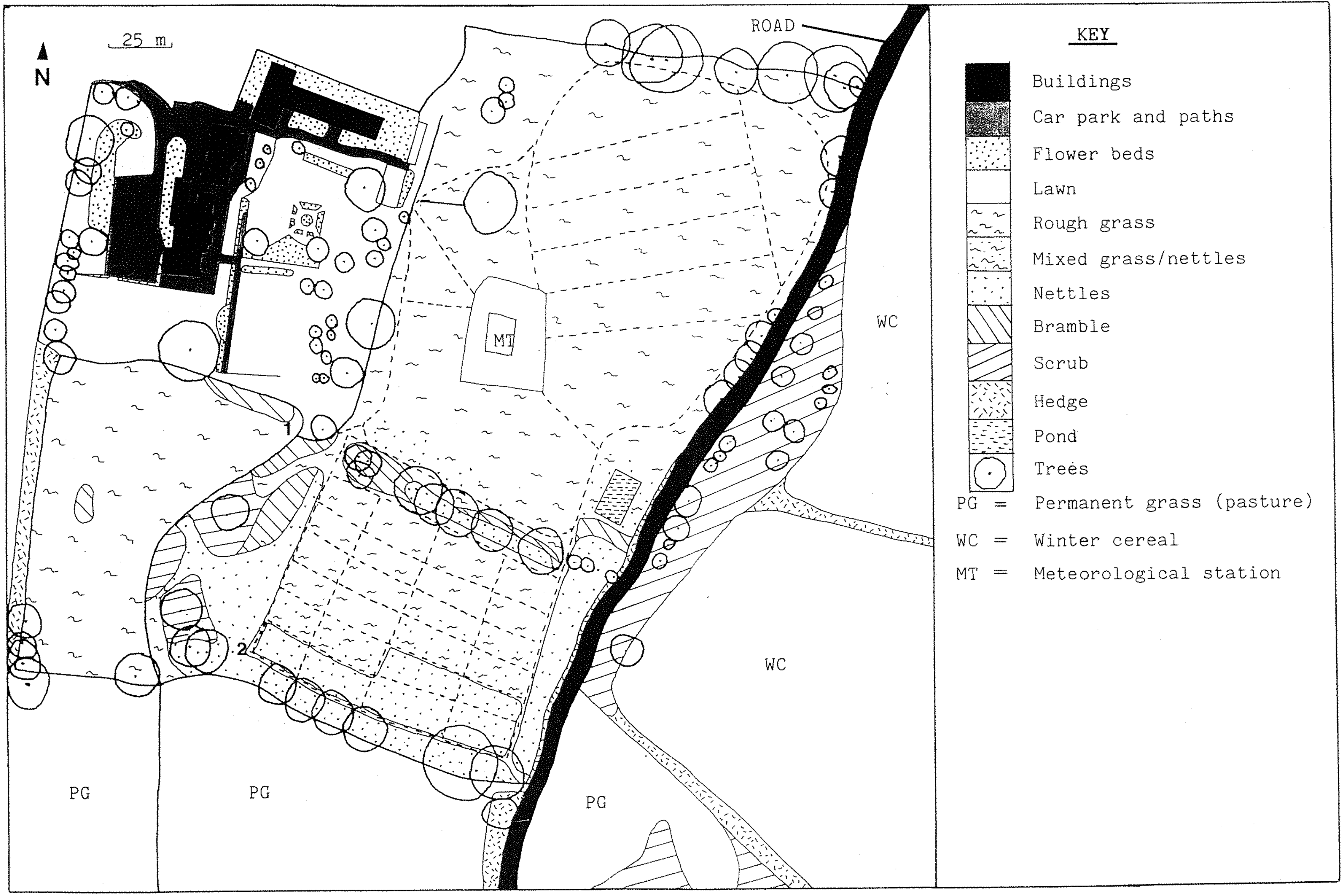


Fig. 2.1. Rogate Field Centre study site and distribution of habitat types, 1985-86.

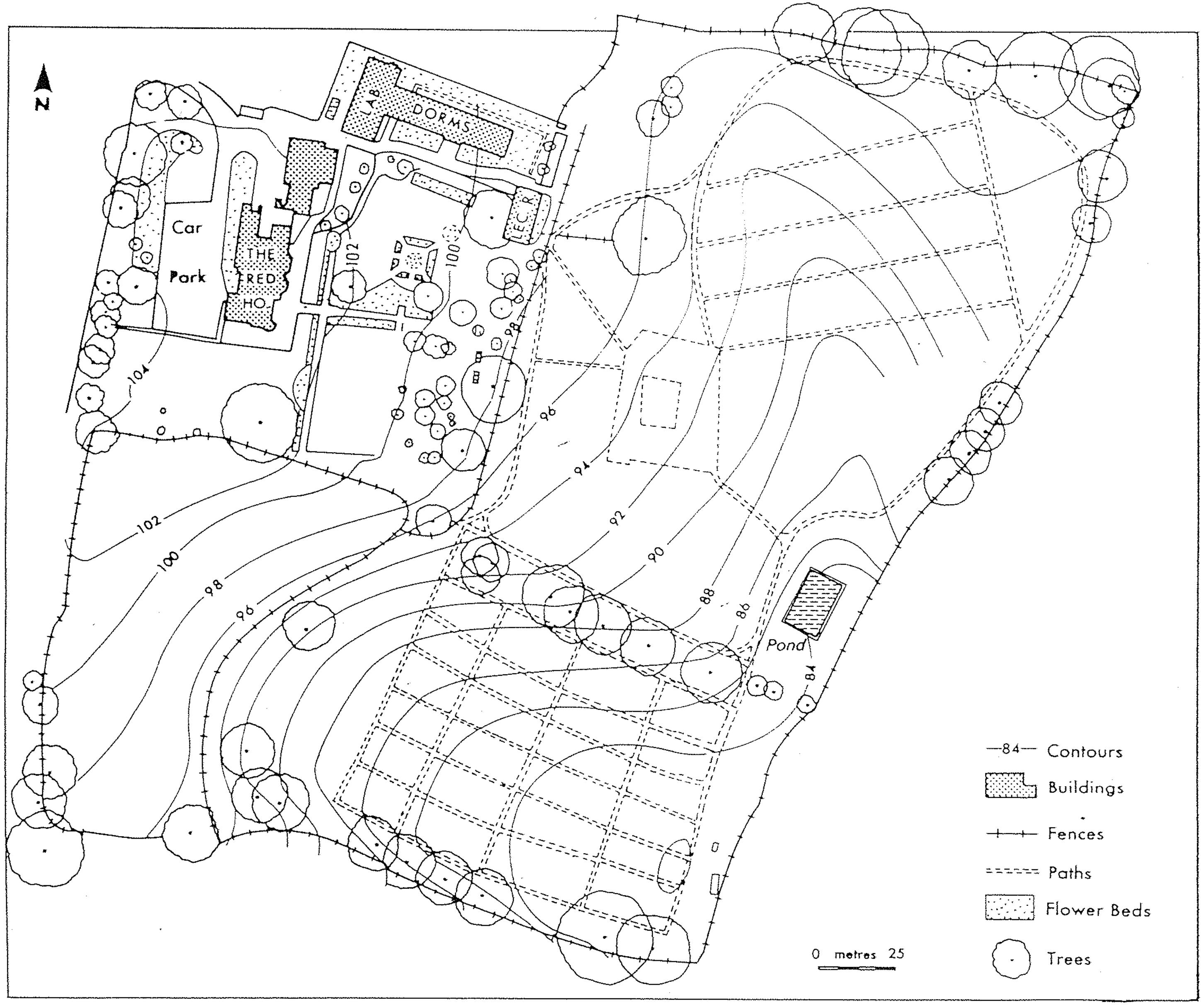


Fig. 2.2. Topography of the Rogate Field Centre study site.

Plate 2.1. South east view of the study site from the north corner of the lower field (location 1 in Fig. 2.1), July 1985.

Plate 2.2. South east view of the study site as Plate 1.1 above, February 1986.

Plate 2.3. North east view of the study site from the lower field (location 2 in Fig. 2.1), July 1985.

Plate 2.4. North east view of the study site as Plate 2.3 above, February 1986.

METHODS

Location of anvils and thrush feeding sites.

The locations of thrush anvils were established in December 1984 by thoroughly searching the entire study site, adjoining hedgerows and copses. Although the anvils were not being used at the time, there were large and conspicuous piles of shell fragments remaining from the previous summer. Observations of feeding thrushes were also made during the snail predation periods to locate any hidden anvil sites; however, no further thrush anvils were located by this method.

In order to locate the main feeding areas of the song thrushes, seven visits were made to the study area between 29th January and 13th March 1985, during which the entire site was searched and the postions of thrushes and their activities mapped. In July 1985 and February 1986 song thrushes were trapped with mist nets and each was ringed with a metal British Trust for Ornithology ring, and two plastic colour rings.

The sites of the anvils used by song thrushes are shown in Fig. 2.3. The anvils numbered 1 to 7 were the main ones used throughout the study period. The anvils denoted with a subsidiary letter are adjacent anvils which were used for short periods only. The anvil totals used in the analysis are the totals of all shell remains from each main anvil and their corresponding adjacent subsidiary anvils. The shell remains were collected at weekly intervals throughout the predation periods, and during the long periods when song thrushes were not feeding on snails the anvils were inspected at 2-3 weekly intervals..

Snails without lips were classed as juveniles, whilst those with partial or complete lips were considered to be adult. Juvenile snails were not counted or included in any analysis because band fusions are often not discernable until the second or third year (Bantock 1971), and therefore reliable identification of *Cepaea* morphs is not possible. Furthermore, the shell remains of juveniles were frequently consisted of shell fragments lacking complete aperture sections. Accurate counting of predated juvenile snails from shell remains was therefore difficult. Adult snails

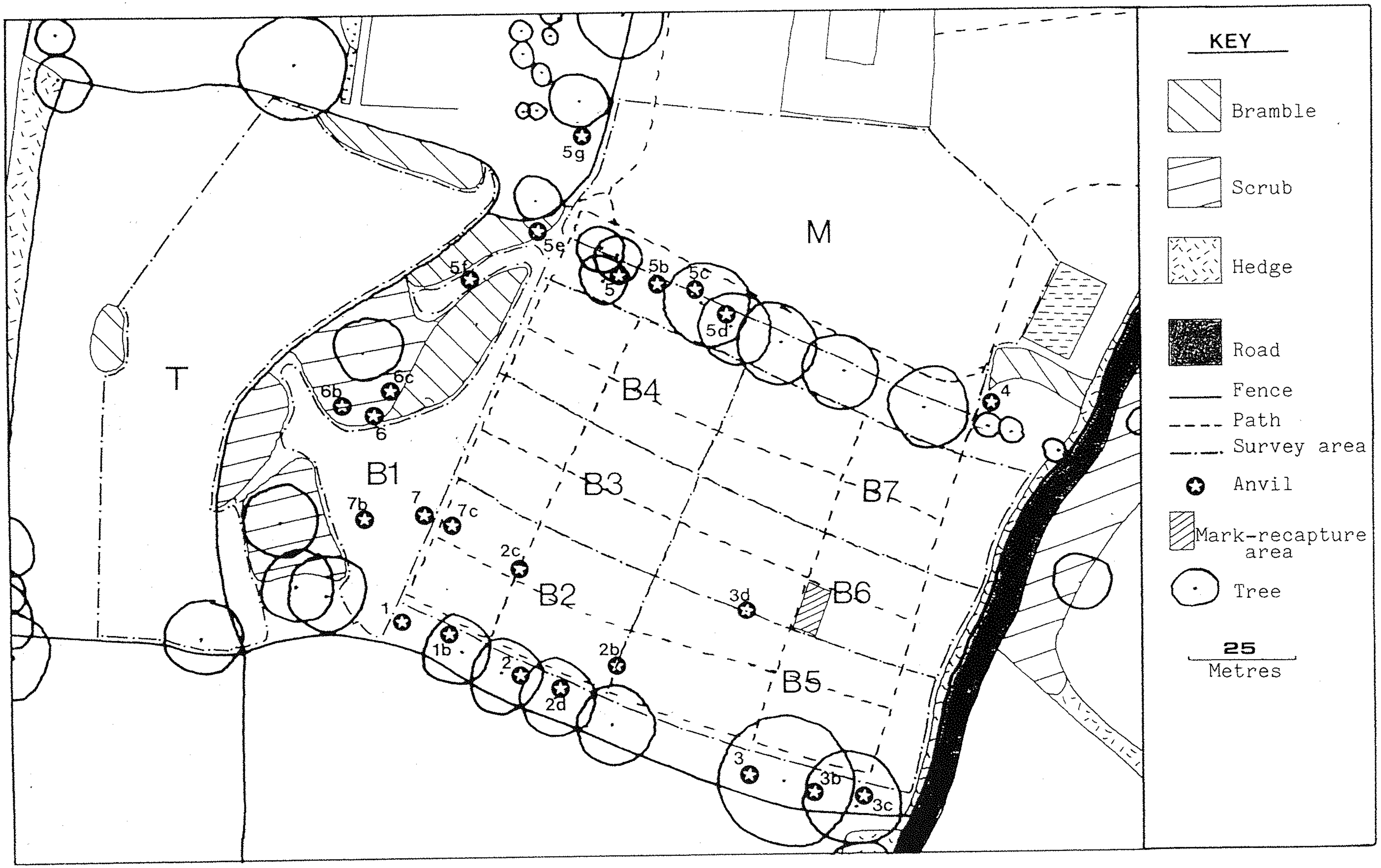


Fig. 2.3. Location of Song Thrush anvils and the extent of the survey areas.

were only counted if more than half the lip was present.

Rabbits (*Oryctolagus cuniculus*) and bank voles (*Clethrionomys glareolus*) are known to feed on snails, and it is possible for the shell remains to occur in the vicinity of thrush anvils. However, shells broken by song thrushes are easily distinguishable from those predated by mammals, because mammals have the habit of breaking open the shell around the spiral (Morris 1954). Definite cases of snail predation by mammals were only found on two occasions at anvil sites. However, shell remains that showed the typical signs of mammal predation were frequently found during the intensive ground searches in the winter surveys (see below).

Cepaea hortensis morph scoring

Following the general scheme of Clarke (1960) the shell colour of unbanded morphs was classified as either yellow, pink or brown. However, brown shells were rare and in some cases difficult to distinguish from pink shells. Analysis was therefore carried out on the combined totals of pink and brown shells. Banded shells were not separated by background colour because reliable assessment of pink and brown shells was often impossible, especially on small shell fragments.

Banding was noted in the conventional way with bands numbered 1, 2, 3, 4, and 5 from the top of the whorl downwards. The usual form of notation is used throughout this thesis, so that fused bands are recorded within brackets (eg. (123)45) and missing bands are recorded as 0. Bands were only classified as fused if they were fused beyond 90° round the whorl from the lip. Throughout the anvil collections and live snail surveys adult snail morphs were recorded as described above. However, for analysis banded snails were classified into four categories as follows:

(1) Five-banded (Y/P5).

Five-banded morphs without fusions and fully pigmented.

(2) Five-banded with fused upper bands (Y/P5-(123)).

Five-banded morphs with at least the upper three bands fused. The most common morphs at Rogate in this category where (123)45 and (12345).

(3) Five-banded, effectively unfused (Y/P5-EUF).

Five-banded morphs with fused bands that did not include all of the upper three bands, so that the snail appears generally banded and without obvious fusions when viewed from above. The most common morphs at Rogate in this category were 1(23)45 and 123(45).

(4) Other banded morphs.

Morphs with missing bands or five-banded morphs with pale (*var. lunaria*) or completely unpigmented bands (*var. arenicola*). All these morphs were extremely rare and therefore are not included in the analysis.

Live snail survey.

The live snail populations were surveyed during each predation period throughout the study. The study site was divided into the survey areas shown in Fig. 2.3. Ten random m^2 quadrat samples were taken in each area during the during the summer surveys, whilst 20 and 17 quadrats were searched in the 1985 and 1985/86 winter surveys respectively. Fewer quadrats were searched in the summer surveys because of the apparently higher densities in that period. The surveys were normally carried out over several days, the dates of which are shown below.

Winter 1985: 22 February, 3 March (total samples = 180).

Summer 1985: 13 August, 20 August, 11 September, 3 October (total samples = 90).

Winter 1985/86: 11 March, 14 March (total samples = 170).

Summer 1986: 16 September (total samples = 90).

The winter surveys were carried out by simply 'haphazardly' throwing the quadrat within each survey area. However, because of the dense vegetation the location of quadrats was determined by the use of random co-ordinates in the summer surveys. All snails found within the quadrat were collected and identified. *Cepaea* morphs were scored and then classified as described above. During the winter surveys the collection of snails was straightforward because of the low vegetation, and snails that were buried up to 30 mm deep were easily found by scraping away the overlying soil. Therefore, the numbers of snails found in quadrats could be reliably used for density estimations. However, the dense structure of the vegetation during the summer surveys made the collection of snails difficult. When disturbed, snails often dropped from the vegetation and fell out of the quadrat. Furthermore, some snails probably remained undetected, especially those on the ground or buried, because destruction and removal of vegetation from each quadrat was not possible. Therefore, although the summer survey provides adequate data for the estimation of frequencies, the calculation of densities is less likely to be valid.

In order to estimate the density of snails during the summer predation period a mark-recapture study was carried out using Bailey´s Triple Catch method (Bailey 1951) within a representative area of the lower study field (see Fig 2.3). Within a 84m^2 (8 X 10.5 m) plot in area B6, collections of adult *Arianta arbustorum* and *Cepaea hortensis* were made on 7 June, 5 July and 9 August. On each visit 150 - 200 adults were collected and on the first two visits each snail was marked by drilling a 0.8 mm hole (with a battery powered modelling drill) through the shell immediately behind the lip. Snails collected on the first visit (7 June) were marked on the upper edge of the whorl, whilst snails collected on the second visit were marked on the lower edge. After marking, each snail was returned to its place of capture. The total number of each species collected and the number previously marked was recorded on each visit.

The effect of drilling on adult snail mortality was assessed by marking ten adults of each species with drill holes in both marking positions, and observing them over the period of the mark-recapture study. The snails were kept in *the laboratory in* perspex tanks with gravel covered floors and ventilated lids at room temperature and in a shaded position. Lettuce was provided every 2-3 days and the tanks were emptied, cleaned and the gravel washed every week. The snails generally remained inactive throughout the period except for immediately after the tanks were cleaned. Over the entire mark-recapture study period, only one adult *Arianta* died. Thus there was no evidence that the drilling adversely affected adult survival.

Meteorological data collection.

Daily meteorological data were collected from the Meteorological Office Weather Station at Rogate Field Centre, for the entire study period. The following weather parameters were collected:

(1) Mean temperature, estimated as (maximum + minimum)/2. Temperature measurements were made with a dry bulb thermometer in a louvered screen 1.21 m above short grass.

(2) Minimum grass temeperature. This is the minimum overnight temperature recorded by a thermometer about 50 mm above the ground and just in contact with the grass. This gives an indication of the severity of ground frost.

(3) Soil temperature. This is the temperature recorded at 300 mm depth at 09.00 GMT.

(4) Rainfall. Total rainfall (measured in millimetres) over 24 h from 00.00 hrs GMT.

For each weather parameter a weekly mean value was calculated for the predation periods and the preceeding and following week of each period. These data were then used in the analysis of the effects of weather conditions on snail predation rates.

RESULTS

Location of snail feeding

Fig. 2.4 shows the position of song thrushes located during site searches in winter 1985. Most thrushes were observed in the south west field and all 5 observations of snail feeding were in this area. These results and the location of actively used anvils (Fig. 2.3) clearly indicate that this field was the main source of snails found at anvils within the study site.

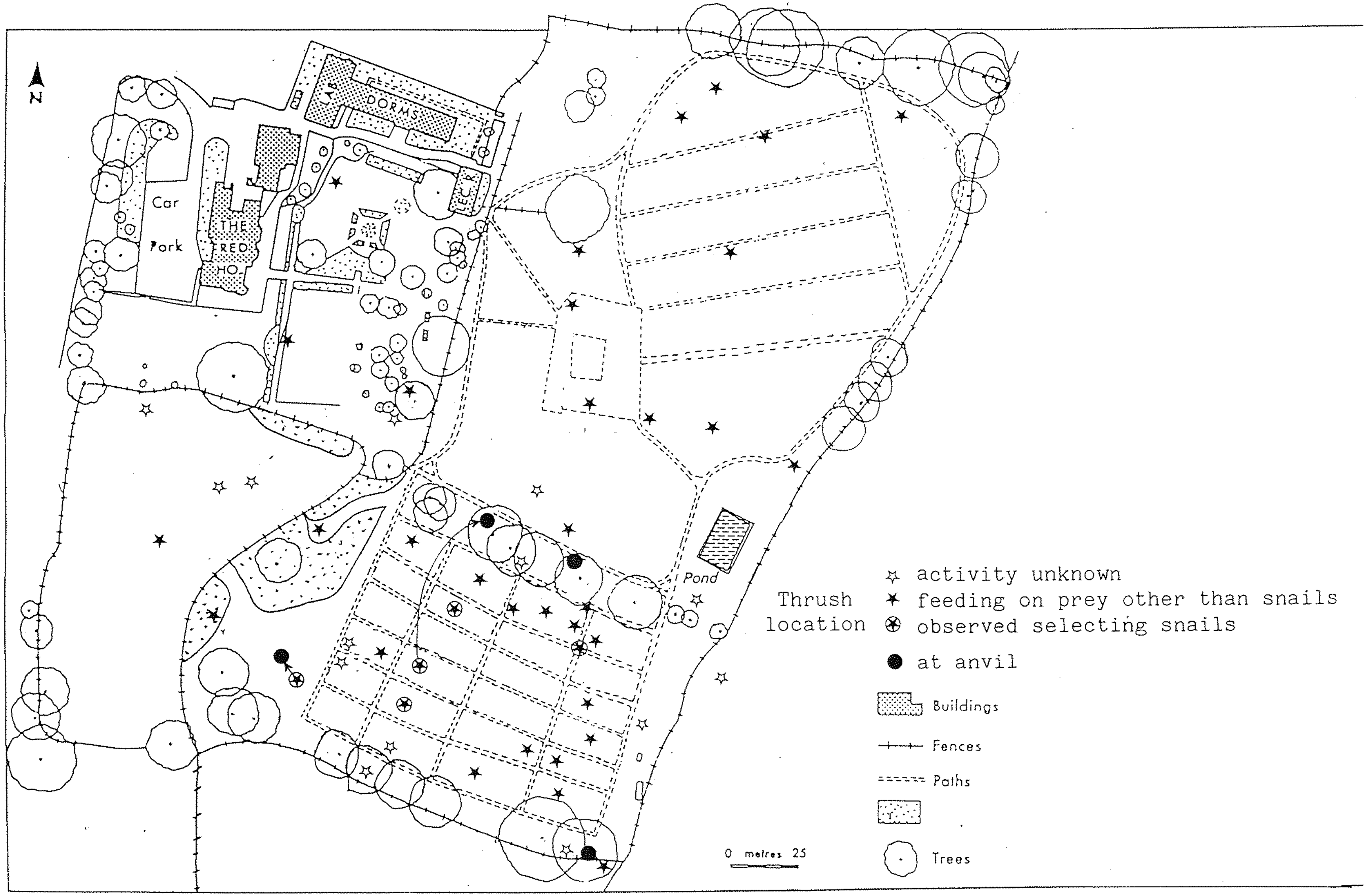


Fig. 2.4. The position of song thrushes located during site searches in winter, 1985.

Thrushes are known to normally carry snails to the nearest available anvil (Sheppard 1951). Therefore, because of the predominance of snail predation in the south west field, the snail surveys were restricted to this field and only the adjoining sections of the adjacent fields (see Fig. 2.3).

Thrushes ringed in the 1985 summer could not be located easily, because of the dense vegetation and vigilance of the birds. Only one bird was definitely re-detected and therefore no useful information was obtained on summer anvil use. During the 1985/86 winter predation period two thrushes were colour ringed on 11 February and two more on 3 March. Again only one bird was re-detected (on 13 February), despite frequent observations until the end of March. Despite the lack of data on anvil use it was clear that there was extensive immigration and emmigration of thrushes through the study site: snail predation was intense throughout the period and song thrushes were always present, with 12 seen feeding on snails on 25 February.

Seasonal variation in snail predation

Four species of snail were found at anvils throughout the study period (January 1985 - October 1986) and the totals recorded at each anvil inspection are presented in Tables 2.1 and 2.2. Remains of juveniles were very rarely found (less than 1% of totals) and are not included in the tables (or in any further analysis of species or morph selection).

Figs. 2.5 and 2.6 are histograms of the data for *Arianta arbustorum* and *Cepaea hortensis*. In each year, predation was clearly restricted to two distinct periods: first, a winter period, with peak predation rates during February, and second a period between mid and late summer, during which predation was greatest in July. Although the two periods covered approximately the same time span, winter predation contributed to the greater proportion of the total number of snails taken throughout the year (71% in 1985 and 81% in 1986). This was probably partly attributable to the higher numbers of thrushes in the study area in winter. The territories of the resident birds are known to breakdown during periods of extremely cold weather (Davies & Snow 1965) and the low temperatures are also associated with an influx

Table 2.1. 1985 weekly predation totals of *Helix aspersa*, *Monacha cantiana*, *Arianta arbustorum* and *Cepaea hortensis* at Rogate, Hampshire.

Anvil inspections started on 8/1/85 and no snail shell remains were found until 29/1.

	Species				
Date	*Helix*	*Monacha*	*Arianta*	*Cepaea*	Total
29/1	1	2	30	67	100
4/2	0	0	3	10	13
12/2	1	2	21	52	76
19/2	4	4	253	294	555
26/2	1	1	273	138	413
5/3	1	0	34	23	58
13/3	0	0	19	10	29
26/3	0	0	20	16	36
2/4	0	0	1	1	2
16/4	0	0	0	3	3
24/4	0	0	1	1	2
Total	6	9	655	615	1285
Percentage	0.47	0.7	51.0	47.8	

No further predation was detected until 4/6/85

4/6	0	0	3	7	10
11/6	0	0	3	8	11
18/6	0	0	4	10	14
25/6	0	0	1	2	3
2/7	0	0	3	25	28
9/7	3	7	49	153	212
16/7	1	3	5	36	45
23/7	4	7	13	36	60
30/7	4	8	13	37	62
6/8	2	3	4	26	35
13/8	2	2	9	12	25
20/8	2	0	9	10	21
Total	18	30	115	362	525
Percentage	3.4	5.7	21.9	68.9	

No further predation was detected until 4/12/85, see Table 2.2

Table 2.2. 1985/1986 weekly predation totals of *Helix aspersa*, *Monacha cantiana*, *Arianta arbustorum* and *Cepaea hortensis* at Rogate, Hampshire.

Species

Date	*Helix*	*Monacha*	*Arianta*	*Cepaea*	Total
4/12/85	2	7	19	26	54
11/12	0	2	5	5	12
7/1/86	4	14	136	90	244
14/1	0	3	38	32	73
21/1	1	5	45	12	63
28/1	2	6	132	40	180
4/2	0	1	78	27	106
11/2	5	7	227	110	349
18/2	9	9	610	480	1108
25/2	6	6	669	575	1256
4/3	8	3	324	353	687
11/3	1	0	85	78	164
18/3	1	0	17	10	28
Total	39	63	2385	1838	4325
Percentage	0.90	1.46	55.1	42.5	

No further predation was detected until 24/6/86

24/6	0	0	1	2	3
2/7	0	0	6	10	16
8/7	8	0	17	70	95
22/7	4	13	115	219	351
29/7	3	7	89	186	285
5/8	1	0	19	46	66
12/8	1	2	31	55	89
19/8	1	1	18	23	43
2/9	1	0	11	9	21
10/9	0	0	17	2	19
Total	19	23	324	622	988
Percentage	1.9	2.3	32.8	63.0	

No further predation was detected upto the last inspection of anvils on 30/9/86.

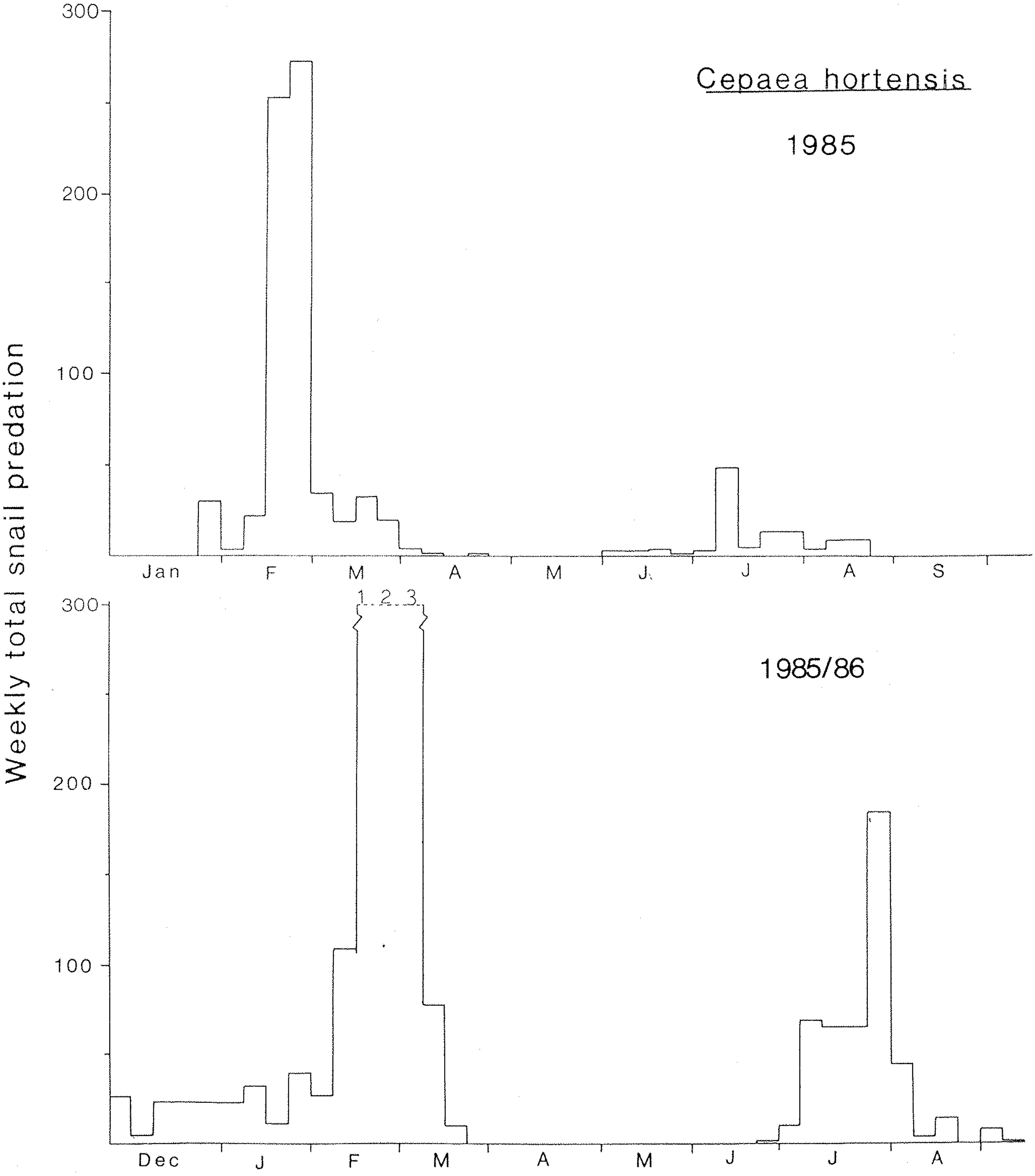


Fig. 2.5. Weekly Cepaea hortensis predation totals at Rogate.
1 = 317, 2 = 575, 3 = 353.

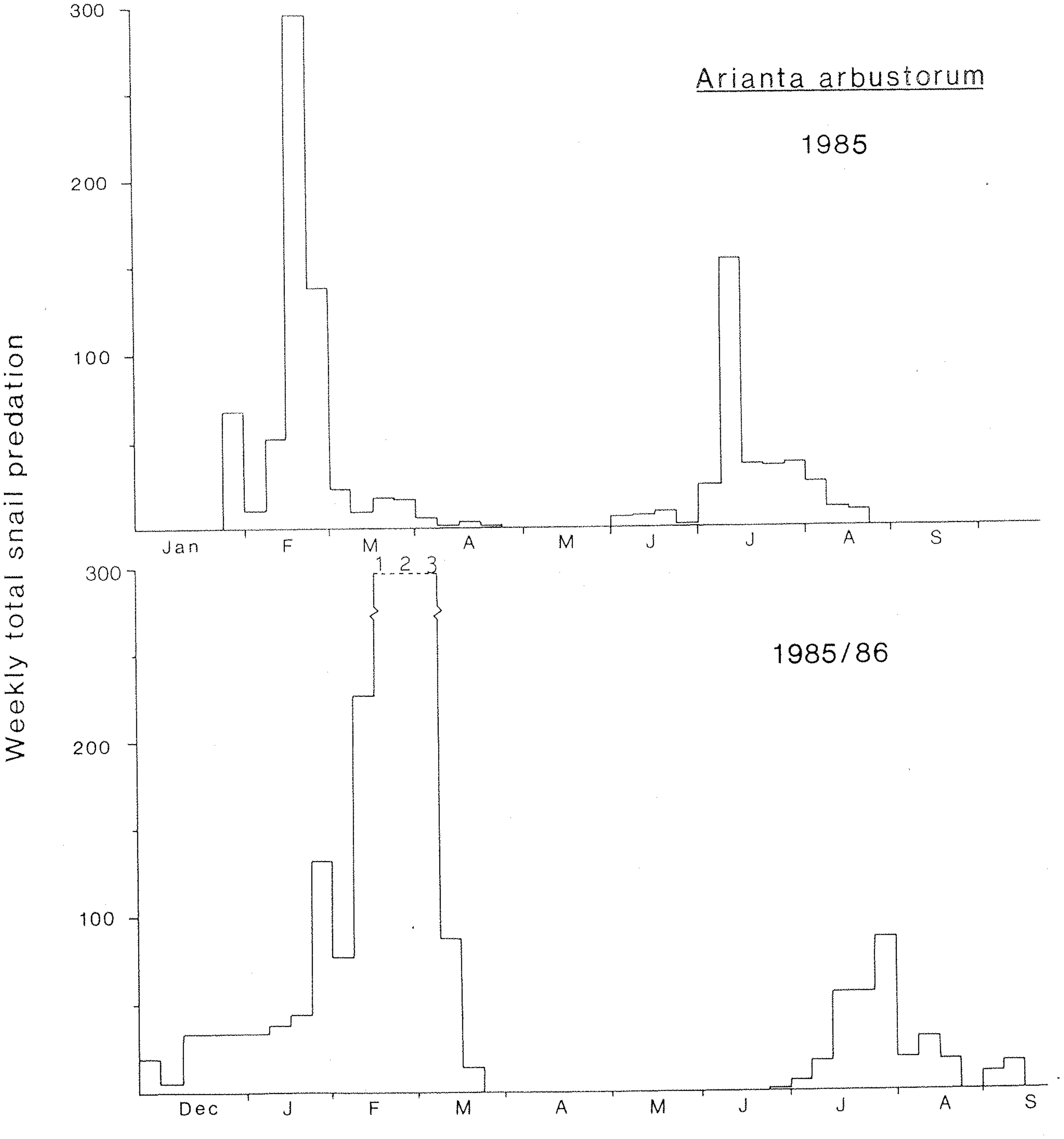


Fig. 2.6. Weekly Arianta arbustorum predation totals at Rogate.
1 = 441, 2 = 669, 3 = 324

of migrants.

From casual observations it appeared that snail predation was restricted to periods of very low temperature during the winter and hot, dry weather in the summer. Similar observations have been made by Goodhart (1958) and Davies & Snow (1965). The effect of weather conditions on snail predation was investigated in detail by correlation and multiple regression of weekly predation totals ($\log_{10}(x+1)$ transformed) against mean weekly weather parameters collected from the meterological station at Rogate Field Centre. Tables 2.3 and 2.4 show the results of the analysis for the winter and the summer periods, with the data from both years combined. For both snail-predation seasons the mean weekly soil temperature (taken at 30cm depth) was the most highly correlated weather parameter with weekly predation level. Furthermore, although other parameters are also significantly correlated, the addition of any of these in the stepwise multiple regression models does not significantly increase the amount of explained variation in predation. Thus the final regression model includes soil temperature as the only significant weather parameter, and this explains 48.4% and 52.0% of variation in winter and summer predation levels respectively. However, the effect of soil temperature is opposite in the two seasons. During the winter, increased predation was correlated with decreased soil temperature (Fig. 2.7), whilst in summer, predation levels were positively correlated with soil temperature. Snail predation thus appears to be restricted to the two extreme periods of soil temperature.

Snail species composition of diet

Tables 2.1 and 2.2 clearly show that *Arianta arbustorum* and *Cepaea hortensis* were the two main species eaten by song thrushes, whilst *Helix aspersa* and *Monacha cantiana* were only taken in small numbers. Furthermore, although the numbers of the latter two species are too low for detailed analysis it is apparent that the relative numbers of *Monacha cantiana* broken at anvils was lower than that expected from the surveys of the live populations (Table 2.5)

These results do not necessarily mean that *Monacha* was **eaten** less than expected, because it is possible that the song thrushes

Table 2.3 Correlation and stepwise multiple regression of winter weekly snail predation with mean weekly weather paramaters.

Pearson Correlation Coeffients

	MT	MGT	ST	R
Mean Temp.				
Min. Grass Temp.	0.862			
Soil Temp	0.815	0.707		
Rainfall	0.407	0.463	0.441	
Snail predation	-0.592	-0.502	-0.723	-0.366

N = 27, Significance levels for the correlation coefficient are: 0.381, $P = 0.05$; 0.487, $P = 0.01$; 0.597, $P = 0.001$

Stepwise Multiple Regression

1 Variable significant at $P > 0.05$: Soil Temperature

Intercept = 3.19
Slope (Soil Temperature) = -0.321 (Standard Error = 0.061)
Total $r^2 = 0.523$
F = 27.4, d.f. = 1,26, $P < 0.001$

Table 2.4 Correlation and stepwise multiple regression of summer weekly snail predation with mean weekly weather paramaters.

Pearson Correlation Coeffients

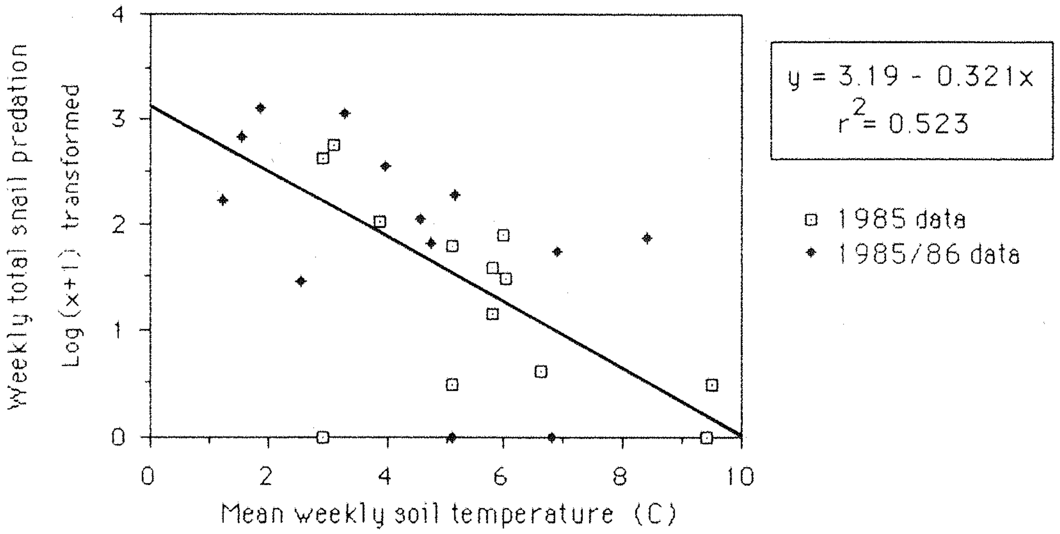
	MT	MGT	ST	R
Mean Temp.				
Min. Grass Temp.	0.635			
Soil Temp	0.743	0.691		
Rainfall	-0.286	0.189	-0.131	
Snail predation	0.474	0.456	0.728	-0.190

N = 26, Significance levels for the correlation coefficient are: 0.381, $P = 0.05$; 0.487, $P = 0.01$; 0.597, $P = 0.001$

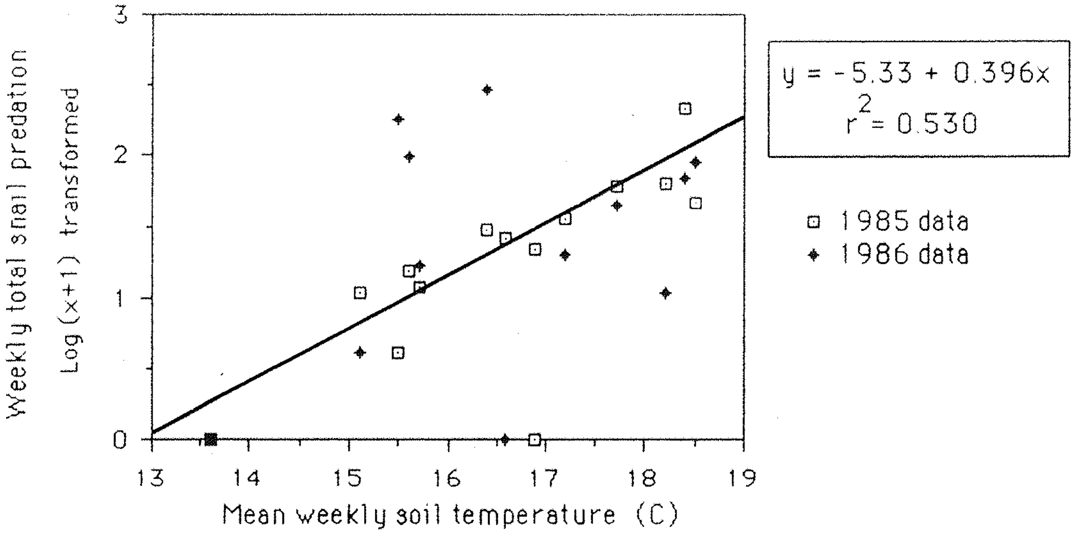
Stepwise Multiple Regression

1 Variable significant at $P > 0.05$: Soil Temperature

Intercept = -5.33
Slope (Soil Temperature) = 0.396 (Standard Error = 0.076)
Total $r^2 = 0.530$
F = 27.1, d.f. = 1,25, $P < 0.001$



a) Winter



b) Summer

Fig. 2.7. The relationship between mean weekly soil temperature and weekly total snail predation during a) winter and b) summer predation periods.

Table 2.5. Predation and survey totals for the landsnails *Helix aspersa*, *Monacha cantiana*, *Arianta arbustorum* and *Cepaea hortensis* at Rogate, Hampshire.

Percentage of predation and survey total are indicated in brackets.

		Species			
		Helix	*Monacha*	*Arianta*	*Cepaea*
1985	Winter				
	Survey	14 (6·1)	47 (20·5)	49 (21·4)	119 (52·0)
	Predated	6 (0.5)	9 (0.7)	655 (51.0)	615 (47.8)
	Summer				
	Survey	1 (0.3)	122 (37.3)	25 (7.6)	179 (54.7)
	Predated	18 (3.4)	30 (5.7)	115 (21.9)	362 (68.9)
1986	Winter				
	Survey	1 (0.3)	26 (8.5)	151 (49.7)	126 (41.4)
	Predated	39 (0.9)	63 (1.5)	2385 (55.1)	1838 (42.5)
	Summer				
	Survey	5 (2.1)	43 (18.2)	35 (14.8)	153 (64.8)
	Predated	19 (1.9)	23 (2.3)	324 (32.8)	622 (63.0)

ate this species of snail without taking them to anvils. Indeed, I observed song thrushes and blackbirds swallowing small snails whole during winter. However, the maximum width of 32 snails seen being swallowed was 10-12 mm (estimated by comparison to song thrush bill size; mean bill length = 14.0 mm, range 13-15 mm, Cramp 1988). It therefore seems unlikely that adult *Monacha* would have been eaten without being taken to an anvil because adult *Monacha cantiana* at Rogate had shell widths greater than 12 mm; mean width = 15.6 mm (standard error = 0.258) from a random sample of 17 adults on 13/8/85.

Large numbers of *Arianta* and *Cepaea* were taken in both predation periods and these data were examined in more detail. In particular, the frequency of each species in the shell remains were simultaneously analysed for heterogeneity within each main predation period and between anvil sites. This analysis was carried out by 3-way log linear modelling (Sokal and Rohlf 1981), which tested the independence of species frequency from anvil site and sub-period, as well as testing for 2-way and 3-way interactions between all variables. This technique is statistically robust and remains valid with expected cell frequencies below 5 and observed cell frequencies of 0 provided they do not occur in more than 1:5 and 1:20 cells respectively. For both winter predation periods each anvil group was treated separately. This was not possible for the summer data, because of the smaller sample sizes; where necessary, data from adjacent anvils were combined. In most predation periods, the data were split into only two sub-periods. The 1985 winter data were split into 3 sub-periods. The results are given in Tables 2.6 to 2.9. In all predation periods except the summer period in 1985, the predated morph frequencies were not independent of sub-period or anvil, and there was significant interaction between all three variables. The 1985 data also shows that there were significant differences between anvils, although there was no difference between early and late predation periods.

These results indicate that it is invalid to combine the predation data from anvils and sub-periods for comparison with the species frequencies obtained from the snail surveys. Although the temporal heterogeneity could be overcome by restricting the analysis to the predation at the time of the live snail surveys,

Table 2.6. 1985 Winter predation of *Arianta arbustorum* and *Cepaea hortensis*.

Period: Early = 4/2/85 - 19/2/85; Late = 20/2/85 - 22/4/85.

		Period		
Anvil	Species	Early	Late	Total
1	Arianta	16	27	43
	Cepaea	31	10	41
2	Arianta	72	78	150
	Cepaea	92	56	148
3	Arianta	38	74	112
	Cepaea	14	37	51
4	Arianta	14	3	17
	Cepaea	43	3	46
5	Arianta	46	59	105
	Cepaea	138	59	197
6	Arianta	91	116	207
	Cepaea	37	41	78
7	Arianta	2	65	67
	Cepaea	1	18	19
Total	Arianta	279	422	699
	Cepaea	356	224	580

Total independence of Species & Month & Anvil; G = 369, d.f. = 19, $P<0.001$

Species independence from Month & Anvil; G = 184 d.f. = 13, $P<0.01$

2-Way tests of independence:

Month x Species; G = 22.5, d.f. = 1, $P <0.001$
Anvil x Species; G = 124 d.f. = 6, $P <0.001$
Month x Anvil; G = 146, d.f. = 12, $P <0.001$

3-Way interaction; G = 18.5, d.f. = 6, $P <0.01$

All G values are Williams corrected.

Table 2.7. 1985 Summer predation of *Arianta arbustorum* and *Cepaea hortensis*.

		Period			
Anvil	Species	Early	Late	Total	% Cepaea
1 & 7	Arianta	1	19	20	
	Cepaea	6	42	48	70.5
2	Arianta	3	10	13	
	Cepaea	8	7	15	53.6
3	Arianta	51	19	70	
	Cepaea	163	42	204	74.4
4	Arianta	3	5	8	
	Cepaea	10	27	37	82.2
5	Arianta	0	5	5	
	Cepaea	6	50	56	91.8
Total	Arianta	58	58	116	
	Cepaea	193	168	361	

Total independence of Species & Period & Anvil; G = 216, d.f. = 13, $P<0.001$

Species independence from Period & Anvil; G = 25.7 d.f. = 9, $P<0.01$

2-Way tests of independence:
Period x Species; G = 2.95, d.f. = 1, $P>0.05$
Anvil x Species; G = 21.7, d.f. = 4, $P <0.001$
Period x Anvil; G = 192, d.f. = 4, $P <0.001$

3-Way interaction; G = 3.39, d.f. = 4, $P >0.05$

All G values are Williams corrected.

Table 2.8. 1985/86 winter predation of *Arianta arbustorum* and *Cepaea hortensis*.

		Month			
Anvil	Species	Dec/Jan	Feb	Mar	Total
1	Arianta	34	148	24	206
	Cepaea	28	100	34	162
	% Cepaea	45.2	40.3	58.6	
2	Arianta	55	377	29	461
	Cepaea	30	454	69	553
	% Cepaea	64.7	54.6	70.4	
3	Arianta	19	225	81	325
	Cepaea	36	240	75	351
	%Cepaea	65.4	51.6	48.1	
4	Arianta	25	37	2	64
	Cepaea	29	68	16	113
	% Cepaea	53.7	64.8	88.9	
5	Arianta	1	39	16	56
	Cepaea	10	157	46	213
	% Cepaea	90.9	80.1	74.2	
6	Arianta	210	333	49	592
	Cepaea	40	87	40	167
	% Cepaea	16.0	20.7	44.9	
7	Arianta	31	425	224	680
	Cepaea	32	86	161	279
	% Cepaea	50.7	16.8	41.8	
Total	Arianta	375	1584	425	2384
	Cepaea	205	1192	441	1838

Total independence of Species & Month & Anvil; G = 1267, d.f. = 32, P<0.001
Species independence from Month & Anvil; G = 636, d.f. = 20, P<0.001

2-Way tests of independence:
Month x Species; G = 57.7, d.f. = 2, P <0.001
Anvil x Species; G = 501.4, d.f. = 6, P <0.001
Month x Anvil; G = 653.7, d.f. = 12, P < 0.001

3-Way interaction; G = 98.7, d.f. = 12, P <0.001

All G values are Williams corrected.

Table 2.9. 1986 summer predation of *Arianta arbustorum* and *Cepaea hortensis*.

Anvil	Species	Period June/July	 Aug/Sep	Total
1	Arianta	13	10	23
	Cepaea	19	13	32
	% Cepaea	59.4	56.5	
2	Arianta	30	6	36
	Cepaea	22	10	32
	% Cepaea	42.3	62.5	
3	Arianta	172	34	206
	Cepaea	297	31	328
	% Cepaea	63.3	47.6	
4+5	Arianta	13	8	21
	Cepaea	147	12	159
	% Cepaea	91.9	60.0	
6	Arianta	23	16	39
	Cepaea	71	28	99
	% Cepaea	75.5	63.6	
Total	Arianta	251	74	325
	Cepaea	556	94	650

Test for complete independence of Species & Period & Anvil; $G = 141.9$, d.f. 13, $P < 0.001$

Species independence from Period & Anvil; $G = 88.4$ d.f. = 9, $P < 0.001$

2-Way tests of independence:
Period x Species; $G = 9.05$, d.f. = 1, $P < 0.01$
Anvil x Species; $G = 64.8$, d.f. = 4, $P < 0.001$
Period x Anvil; $G = 51.9$, d.f. = 4, $P < 0.001$

3-Way interaction; $G = 13.2$, d.f. = 4, $P < 0.01$

All G values are Williams corrected.

this does not take account of the heterogeneity between anvils. The orginal location of the snails taken to the anvils is not known, and therefore individual anvils cannot be justifiably compared with specific survey areas. Therefore, these data cannot be used for investigation of selection of *Arianta arbustorum* and *Cepaea hortensis*; it is not valid to compare species frequencies in the shell remains with the species frequencies calculated from the surveys of live snails. Furthermore, comparison of species selection between seasonal periods of predation is impossible: there are significant 3-way interactions in three out of the four periods.

The observed heterogeneity in frequency of *Arianta arbustorum* and *Cepaea hortensis* remains among anvils could have been caused by (a) different selection by individual birds using different anvils, (b) spatial variation in the relative availability of the snail species within the study site, (c) both of these. The first cause could not be easily tested in this study. Differences in the availability of adult snails could, however, be examined by analysing the survey data for differences in species frequencies between survey areas. However, in the two summer surveys and the 1985 winter survey, the survey areas had to be combined, because the sample sizes for each individual area were so small. The data were pooled by combining adjacent survey areas, i.e. B1 was combined with the adjacent B2 and B3 (see Fig. 2.3), M was combined with B4 and B7, thus leaving B5 and B6 to form a third group. G-tests were then used to test for heterogeneity between the grouped survey areas. With the exception of the 1985 summer survey there were significant differences in the frequencies of the species between survey areas (Table 2.10). Thus, the differences in species frequencies between anvils was at least partially attributable to differences in the availability of the two species within the study site.

***Cepaea hortensis* morph predation**

To test for morph selection, the data for predation on adult *Cepaea* were first examined for heterogeneity among anvils and sub-periods in each main predation period. The data from adjacent anvil groups was combined where necessary (i.e. when the cell frequency requirements for 3-way tables stated above were not met)

Table 2.10. Total numbers of adult *Arianta arbustorum* and *Cepaea hortensis* found in each survey area, in all surveys.

			Survey area							
Year	Season	Species	B1	B2	B3	B4	B5	B6	B7	M
1985	Winter	Arianta	6	15	13	0	4	2	4	5
		Cepaea	6	11	20	4	22	13	16	22
		% Cp	50.0	42.3	60.6	-	84.6	86.7	80.0	81.5
1985	Summer	Arianta	0	4	1	0	1	18	1	0
		Cepaea	1	24	10	16	42	63	22	1
		% Cp	-	85.7	90.9	100	97.7	77.8	95.6	-
85/86	Winter	Arianta	29	23	24	5	30	23	10	5
		Cepaea	5	14	31	6	18	24	16	15
		% Cp	14.7	37.8	56.4	54.5	37.5	51.1	61.5	75.0
1986	Summer	Arianta	2	3	5	10	0	3	3	0
		Cepaea	13	37	24	16	9	46	8	9
		% Cp	86.7	92.5	82.7	61.5	-	93.9	72.7	-

G-Tests for independence within each survey.

1985 - Winter (grouped data): G = 21.8, d.f. = 7, **P** <0.01
1985 - Summer (grouped data): G = 5.85, d.f. = 2, P >0.05
1985/86 - Winter: G = 29.5, d.f. = 7, **P** <0.001
1986 - Summer (grouped data): G = 11.1, d.f. = 2, **P** <0.01

Summer grouped data: 1 = B1,B2,B3; 2 = B5,B6; 3 = B4,B7,M.
All G values are Williams corrected.

and each predation period was split into two sub-periods. Tables 2.11 to 2.14 summarize the predation of each morph and present the results of the 3-way tests of independence. In all predation periods except during the 1985/86 winter, morph predation was independent of sub-period and anvil group. During the 1985/86 winter there were significant differences among anvils but there was no difference between the sub-periods.

Comparisons were then made of morph selection between winter and summer for both years. Since there was no heterogeneity among sites in the 1985 data, the morph totals from the two predation periods were combined. There was a significant difference between the winter 1985 and summer 1985 predation of *Cepaea* morphs (Table 2.15), and this was attributable to the Y/P5 and Y/P5-(123) morphs. The former were eaten significantly less frequently and the latter more frequently in the summer. The 1985/86 data were also examined for seasonal differences in morph selection. However, because of heterogeneity among anvil groups in the winter data, anvils were not combined for the analysis (except for anvil groups 1,2 and 7 in the summer data, because of small sample sizes). There was no significant heterogeneity among these anvil groups in the winter data ($G = 11.2$, d.f. $= 8$, $P > 0.05$). Table 2.16 presents the results of the 3-way log linear analysis. In contrast to the 1985 data there was no significant difference in morph selection between season. Furthermore, there is no clear trend in the direction of change in either the Y/P5-(123) morph or any other morph between the anvil groups. Therefore, these results suggest that there was no consistent difference in morph selection between winter and summer predation periods.

Each survey period was analysed for morph selection with respect to availability. Data were combined for all anvils and sub-periods where heterogeneity was absent. Examination of the live snail survey data also showed that for each season and year, there was no significant heterogeneity between survey areas (Table 2.17). This further confirms the validity of combining the predation data from anvil sites for all periods except the 1985/86 winter predation data (where significant heterogeneity was present). Comparison of the snail surveys also shows that although there were significant differences among morph frequencies between seasons, (Table 2.18), these differences were consistent between

Table 2.11. 1985 winter predation of *Cepaea hortensis*; morph selection.

Period: Early = 4/2/85 - 19/2/85; Late = 20/2/85 - 16/4/85.
Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

		Period			
Anvil	Morph	Early	Late	Total	
1 & 7	YU	5	2	7	
	PU	11	12	23	
	Y/P5	11	5	16	
	Y/P5-(123)	0	3	3	
	Y/P5-EUF	3	4	7	
2	YU	17	3	20	
	PU	25	23	48	
	Y/P5	32	16	48	
	Y/P5-(123)	6	4	10	
	Y/P5-EUF	8	9	17	
3	YU	1	8	9	
	PU	7	10	17	
	Y/P5	3	14	17	
	Y/P5-(123)	0	1	1	
	Y/P5-EUF	2	3	5	
4 & 5	YU	25	3	28	
	PU	63	20	83	
	Y/P5	49	27	76	
	Y/P5-(123)	14	3	17	
	Y/P5-EUF	25	9	34	
6	YU	4	2	6	
	PU	18	16	34	
	Y/P5	10	16	26	
	Y/P5-(123)	2	3	5	
	Y/P5-EUF	2	2	4	
					%
Total	YU	52	18	70	12.5
	PU	124	81	205	36.5
	Y/P5	105	78	183	32.6
	Y/P5-(123)	22	14	36	6.42
	Y/P5-EUF	40	27	67	11.9

Total independence of Morph, Period and Anvil; G = 91.4, d.f. = 40, **P <0.001**
Morph independence from Period & Anvil; G = 44.9, d.f. = 36, P >0.05

2-Way test of independence:
Period x Anvil; G = 49.0, d.f. = 4, **P <0.001**

All G values are Williams corrected.

Table 2.12. 1985 summer predation of *Cepaea hortensis*; morph selection.

Period: Early = 4/6/85 - 9/7/85; Late = 9/7/85 - 20/8/85.
Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

		Period			
Anvil	Morph	Early	Late	Total	%
1,2 & 6	YU	2	3	5	
	PU	3	25	28	
	Y/P5	4	16	20	
	Y/P5-(123)	2	3	5	
	Y/P5-EUF	3	4	7	
3	YU	21	6	27	
	PU	55	18	73	
	Y/P5	36	7	43	
	Y/P5-(123)	16	5	21	
	Y/P5-EUF	30	5	35	
4 & 5	YU	1	7	8	
	PU	3	21	24	
	Y/P5	6	26	32	
	Y/P5-(123)	3	10	13	
	Y/P5-EUF	3	12	15	
Total	YU	24	16	40	11.2
	PU	61	64	125	35.1
	Y/P5	46	49	95	26.7
	Y/P5-(123)	21	18	39	10.9
	Y/P5-EUF	36	21	57	16.0

Total independence of Morph, Period and Anvil; G = 156, d.f. = 22, P <0.001

Morph independence from Period & Anvil; G = 18.5 d.f. = 14, P>0.05

2-Way test of independence:
Period x Anvil; G = 133, d.f. = 2, P <0.001

All G values are Williams corrected.

Table 2.13. 1985/86 winter predation of *Cepaea hortensis*; morph selection.

Period: Early = 4/12/85 - 4/2/86; Late = 4/2/86 - 18/3/86
Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

		Period			
Anvil	Morph	Early	Late	Total	%
1	YU	4	13	17	10.6
	PU	7	39	46	28.7
	Y/P5	11	47	58	36.2
	Y/P5-(123)	2	13	15	9.37
	Y/P5-EUF	6	18	24	15.0
2	YU	3	75	78	14.5
	PU	13	140	153	28.5
	Y/P5	13	183	196	36.5
	Y/P5-(123)	3	38	41	7.63
	Y/P5-EUF	6	63	69	12.8
3	YU	10	55	65	18.8
	PU	14	103	117	33.9
	Y/P5	12	82	94	27.2
	Y/P5-(123)	4	19	23	6.67
	Y/P5-EUF	2	44	46	13.3
4 & 5	YU	12	43	55	16.8
	PU	13	87	100	30.5
	Y/P5	11	91	102	31.1
	Y/P5-(123)	5	20	25	7.62
	Y/P5-EUF	2	44	46	14.0
6	YU	3	16	19	11.6
	PU	26	48	74	45.4
	Y/P5	10	34	44	27.0
	Y/P5-(123)	1	12	13	7.97
	Y/P5-EUF	1	12	13	7.97
7	YU	2	19	21	7.83
	PU	11	83	94	35.1
	Y/P5	10	88	98	36.6
	Y/P5-(123)	1	17	18	6.72
	Y/P5-EUF	8	29	37	13.8

Total independence of Morph, Period and Anvil; G = 113, d.f. = 49, **P <0.001**
Morph independence from Period & Anvil; G = 71.5, d.f. = 44, **P<0.001**

2-Way tests of independence:
Period x Morph; G = 1.7, d.f. = 4, P >0.05
Anvil x Morph; G = 43.6, d.f. = 20, **P <0.01**
Period x Anvil; G = 40.6, d.f. = 5, **P < 0.001**

3-Way interaction; G = 24.6, d.f. = 20, P >0.05

Table 2.14. 1986 summer predation of *Cepaea hortensis*; morph selection.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

		Period			
Anvil	Morph	June/July	Aug/Sept	Total	
1 & 2	YU	4	1	5	
	PU	10	12	22	
	Y/P5	17	7	24	
	Y/P5-(123)	3	2	5	
	Y/P5-EUF	5	1	6	
3	YU	45	4	49	
	PU	98	17	115	
	Y/P5	86	12	98	
	Y/P5-(123)	13	2	15	
	Y/P5-EUF	52	6	58	
4 & 5	YU	26	3	29	
	PU	44	4	48	
	Y/P5	46	3	49	
	Y/P5-(123)	9	1	10	
	Y/P5-EUF	20	1	21	
6	YU	6	3	9	
	PU	28	14	42	
	Y/P5	22	7	29	
	Y/P5-(123)	8	3	11	
	Y/P5-EUF	6	2	8	
					%
Total	YU	81	11	92	14.1
	PU	180	47	227	34.8
	Y/P5	171	29	200	30.6
	Y/P5-(123)	33	8	41	6.28
	Y/P5-EUF	83	10	93	14.2

Total independence of Morph, Period and Anvil; G = 69.9, d.f. = 31, **P<0.001**

Morph independence from Period & Anvil; G = 26.0, d.f. = 16, P>0.05

2-Way tests of independence:
Period x Anvil; G = 37.0, d.f. = 3, **P<0.001**

3-Way interaction; G = 4.17, d.f. = 12, P>0.05

All G values are Williams corrected.

Table 2.15. *Cepaea hortensis* morph selection; comparison between winter 1985 and summer 1985 predation samples.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

	Period					
	Winter		Summer		Haberman´s	
Morph	No.	%	%	No.	stastic	P
YU	70	12.4	11.2	40	-0.56	>0.05
PU	205	36.5	35.1	125	-0.44	>0.05
Y/P5	183	32.6	26.7	95	-1.91	**<0.05**
Y/P5-(123)	36	6.42	10.9	39	2.44	**<0.05**
Y/P5-EU	67	11.9	16.0	57	1.76	>0.05

Morph independence from season; Total $\chi^2 = 11.1$, d.f. = 4, P **<0.05**

Haberman´s statistic: significance levels = standardised normal deviate (Haberman (1973)).

Table 2.16. Comparison of *Cepaea hortensis* morph selection between winter 1985/86 and summer 1986 predation samples.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

		Season			
Anvil	Morph	Winter	%	Summer	%
1,2 & 7	YU	195	24.5	5	8.06
	PU	199	25.0	22	35.5
	Y/P5	254	31.9	24	38.7
	Y/P5-(123)	56	7.02	5	8.06
	Y/P5-EUF	93	11.7	6	9.68
3	YU	65	18.8	49	14.2
	PU	117	33.9	115	33.3
	Y/P5	94	27.2	98	28.4
	Y/P5-(123)	23	6.67	15	4.35
	Y/P5-EUF	46	13.3	58	16.8
4 & 5	YU	55	16.8	29	18.5
	PU	100	30.5	48	30.6
	Y/P5	102	31.1	49	31.2
	Y/P5-(123)	25	7.62	10	6.37
	Y/P5-EUF	46	14.0	21	13.4
6	YU	19	11.6	9	9.09
	PU	74	45.4	42	42.4
	Y/P5	44	27.0	29	29.3
	Y/P5-(123)	13	7.97	11	11.1
	Y/P5-EUF	13	7.97	8	8.1

Total independence of Morph, Season and Anvil; G = 467, d.f. = 31, **P <0.001**

Morph independence from Season & Anvil; G = 80.4, d.f. = 28, **P <0.001**

2-Way tests of independence:
Season x Morph; G = 5.6, d.f. = 4, P > 0.05
Anvil x Morph; G = 50.6, d.f. = 12, **P <0.001**
Season x Anvil; G = 356, d.f. = 3, **P <0.001**

3-Way interaction; G = 13.3, d.f. = 12, P >0.05

All G values are Williams corrected.

Table 2.17. Total numbers of *Cepaea hortensis* morphs found in each survey area, in all surveys.

Winter 1985 Survey area

Morph	B1	B2	B3	B4	B5	B6	B7	M	Total	%
YU	0	2	3	0	2	1	3	2	13	11.9
PU	4	2	2	2	6	2	4	5	28	25.7
Y/P5	2	5	12	2	9	8	6	10	56	51.4
Y/P5-(123	0	0	2	0	0	0	0	1	3	2.75
Y/P5-EUF	0	1	0	0	2	1	1	4	9	8.26

Summer 1985

Morph	B1	B2	B3	B4	B5	B6	B7	M	Total	%
YU	0	4	0	2	12	11	3	0	32	20.8
PU	1	5	2	7	13	24	10	1	63	40.9
Y/P5	0	5	4	5	7	15	5	0	41	26.6
Y/P5-(123)	0	2	1	0	2	1	1	0	7	4.54
Y/P5-EUF	0	4	0	0	1	5	1	0	11	7.14

Winter 1986

Morph	B1	B2	B3	B4	B5	B6	B7	M	Total	%
YU	0	1	4	0	2	2	1	2	14	11.2
PU	4	2	14	3	4	4	6	5	42	33.6
Y/P5	1	10	11	2	9	12	5	6	56	44.8
Y/P5-(123)	0	0	1	0	0	0	0	0	1	0.80
Y/P5-EUF	0	1	0	1	2	3	3	2	12	9.60

Summer 1986

Morph	B1	B2	B3	B4	B5	B6	B7	M	Total	%
YU	1	9	7	4	3	11	3	0	38	20.9
PU	7	9	12	3	2	17	1	5	56	30.8
Y/P5	3	16	16	7	2	26	2	1	73	40.1
Y/P5-(123)	1	1	0	0	1	1	0	0	4	2.20
Y/P5-EUF	1	0	1	3	0	3	1	2	11	6.04

Chi square tests on grouped area data, excluding Y/P5-(123) and Y/P5-EUF.

Groups are: 1 = B1,B2,B3; 2 = B5,B6; 3 = B4,B7,M.

Winter 1985; $X^2 = 1.12$, d.f. = 4, $P > 0.05$
Summer 1985; $X^2 = 4.11$, d.f. = 4, $P > 0.05$
Winter 1985/86; $X^2 = 4.09$, d.f. = 4, $P > 0.05$ (2 cells with expecteds < 5; combined X^2 contribution = 0.067)
Summer 1986; $X^2 = 0.67$, d.f. = 4, $P > 0.05$

Table 2.18. Comparison of *Cepaea hortensis* morph ratios obtained in surveys in each year and season.

		Season			
Year	Morph	Winter	%	Summer	%
1985	YU	13	11.9	32	20.8
	PU	28	25.7	63	40.9
	Y/P5	56	51.4	41	26.6
	Y/P-(123)	3	2.75	7	4.54
	Y/P-EUF	9	8.26	11	7.14
1986	YU	14	11.2	38	20.9
	PU	42	33.6	56	30.8
	Y/P5	56	44.8	73	40.1
	Y/P-(123)	1	0.80	4	2.20
	Y/P-EUF	12	9.60	11	6.04

Total independence of Morph, Season and Year; G = 29.2, d.f = 13, P <0.01

Species independence from Season and Year; G = 29.4, d.f. = 12, P <0.01

Morph x Year; G = 3.78, d.f. = 4, P >0.05
Morph x Season; G = 17.5, d.f. = 4, P <0.01

3-Way interaction; G = 7.82, d.f. = 4, P >0.05

All G values are Williams corrected.

years. Clearly, the differences between seasons indicate that the interpretation of seasonal variation in morph predation is difficult, and therefore straightforward comparisons of shell remains between seasons is unhelpful.

The results of a comparison between winter morph predation and morph availability in 1985 are presented in Table 2.19. The frequency of predated *Cepaea* morphs were significantly different from the frequency available in the winter period, and this was attributable to selection on the PU and Y/P5 morphs. Thrushes took a significantly higher proportion of pink unbanded and a lower proportion of five banded morphs than expected. Because of the anvil heterogeneity the 1985/86 data could not be compared in this way.

Comparison of the morph frequencies of summer predated snails with those available shows that in both years the differences were significant (Tables 2.20 and 2.21). In both years the yellow unbanded morphs were taken significantly less often than expected, whilst the five-banded fused morphs (upper three bands fused) were taken relatively more often than expected . In 1985 the five banded (unfused) morphs were predated significantly less often than expected, whilst the effectively unfused five-banded morphs were predated more often than expected. In 1986 both morphs with fused bands were eaten significantly more often than expected.

Although these results have demonstrated discrepancies between the proportions of morphs eaten and those available, they provide no information on the underlying mechanism creating this effect. Past studies have invoked selective predation by song thrushes based on the visual properties of the shells (Sheppard 1951; Goodhart 1958; Wolda 1963; Carter 1968a). My results can be similarly explained, and this will be discussed later. However, some studies have demonstrated differences in the behaviour of *Cepaea hortensis* morphs (Wolda 1963; Jones 1982). If morphs differ in activity levels and climbing behaviour then this could affect their relative conspicuousness and accessibility to song thrushes. At present there is very little information available on climbing behaviour and how this might affect the risk of predation.

Table 2.19 1985 winter predation of Cepaea; comparison of morph selection with availability.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

	Available		Predated		Haberman's	
	%	sample	No.	%	statistic	P
YU	11.8	13	70	12.5	0.19	>0.05
PU	25.4	28	205	36.5	2.23	**<0.05**
Y/P5	50.9	56	183	32.6	-3.66	**<0.01**
Y/P5-(123)	2.73	3	36	6.42	1.51	>0.05
Y/P5-EUF	9.09	10	67	11.9	0.86	>0.05

Total χ^2 = 14.7, d.f. = 4, **P <0.01**

Haberman's statistic: significance levels = standard normal deviate (Haberman (1973)).

Table 2.20 1985 summer predation of Cepaea; comparison of morph selection with availability.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

	Available		Predated		Haberman's	
	%	sample	No.	%	statistic	P
YU	17.9	32	40	11.2	-2.12	**<0.05**
PU	35.2	63	125	35.1	-0.02	>0.05
Y/P5	33.5	60	95	26.7	-1.64	>0.05
Y/P5-(123)	3.35	6	39	10.9	2.99	**<0.01**
Y/P5-EUF	10.0	18	57	16.0	1.87	>0.05

Total X^2 = 17.01, d.f. = 4, **P <0.01**

Haberman's statistic: significance values = standard normal deviate (Haberman (1973)).

Table 2.21. 1986 summer predation of *Cepaea hortensis*; comparison of morph selection with availability.

Morphs: YU, Yellow unbanded; PU, Pink unbanded; Y/P5, 5-banded without fusions; Y/P5-(123), 5-banded with bands 123 fused; Y/P5-EUF, 5-banded and effectively unfused (bands 123 unfused).

	Available		Predated		Haberman's	
	%	sample	No.	%	statistic	P
YU	28.1	38	92	14.1	-2.23	**<0.05**
PU	41.5	56	227	34.7	1.01	>0.05
Y/P5	54.1	73	200	30.6	-2.41	**<0.05**
Y/P5-(123)	2.96	4	41	6.28	2.16	**<0.05**
Y/P5-EUF	8.15	11	93	14.2	2.96	**<0.05**

Total X^2 = 20.9, d.f. = 4, **P <0.001**

Haberman's statistic: significance values = standard normal deviate (Haberman (1973)).

Snail population estimates and the proportion predated.

The results of the mark-recapture release study are presented in Table 2.22. The estimated densities were 3.00 m^{-2} for *Arianta arbustorum* and 9.58 m^{-2} for *Cepaea hortensis*. Assuming a uniform snail density throughout the study site then the approximate total populations would be 49900 for *Arianta* and 159000 for *Cepaea*. A uniform density is of course, extremely unlikely. In fact, although the summer survey could not provide accurate absolute density estimates, the results clearly indicate that the *Cepaea* populations were not uniformly distributed (Table 2.17). Similar results were obtained from comparisons of *Arianta* numbers collected in the different survey areas. Therefore, it is clear that the extrapolation of the mark-recapture density estimates to the whole study site is invalid.

The density estimates calculated from the 1985/86 winter snail survey are shown in Table 2.23, together with the 95% confidence limits for the population of each survey area. Based upon the population confidence limits, winter predation by song thrushes accounted for 12.4-25.1% of the initial (i.e. estimated population totals + predated totals) *Cepaea hortensis* and 15.8-35.9% of the *Arianta arbustorum* winter populations.

It is clear from the mark-recapture results and winter survey that in area B6 the adult *Cepaea* and *Arianta* populations were substantially larger in the summer. Furthermore, if it is assumed that the relative proportions of snails in each survey area in the winter survey were comparable with those of the summer, then approximate estimates for the summer snail populations can be made. Area B6 contained 19.6% of the total *Cepaea* and 15.1% of the total *Arianta* populations. Therefore, based upon these proportions the summer populations extrapolated from the mark-recapture population estimate for area B6 are approximately 76100 and 30900 for *Cepaea hortensis* and *Arianta arbustorum* respectively. Thus song thrush predation accounted for approximately 0.47% of the *Cepaea* and 0.37% of the *Arianta* summer population in 1985. Although these figures are extremely approximate, they clearly indicate that overall the proportion of snails predated by song thrushes was substantially greater during the winter in this particular year. Consequently, song thrush selection is more

Table 2.22. *Arianta arbustorum* and *Cepaea hortensis* density and population size estimates from a mark-recapture study carried out between 7 June and 9 August, 1985.

Population estimated in a 10.5 x 8m plot (84m^2) within area B6.

Arianta arbustorum

	Capture 1	 2	 3
Date	7 June	5 July	9 August
Total caught	73	35	48
Unmarked	73	27	29
1st mark	-	8	11
2nd mark	-	-	5
1st & 2nd mark	-	-	3

Population estimates:

Total population = 252
Variance = 16750
Emmigration/death rate = -0.916 day^{-1}
Immigration/birth rate = 3.80 day^{-1}
Density = 3.00m^{-2}

Cepaea hortensis

	Capture 1	 2	 3
Date	7 June	5 July	9 August
Total caught	139	124	90
Unmarked	139	99	56
1st mark	-	25	18
2nd mark	-	-	12
1st & 2nd mark	-	-	4

Population estimates:

Total population = 805
Variance = 90590
Emmigration/death rate = -2.24 day^{-1}
Immigration/birth rate = 3.75 day^{-1}
Density = 9.58m^{-2}

Table 2.23. *Arianta arbustorum* and *Cepaea hortensis* density and population size estimates from the 1985/86 winter live snail survey.

Mean and standard error (S.E.) estimates are based upon Log(x+1) tranformed data. N = 17 for each area. Population size confidence limits are based upon derived mean densities and standard errors.

Arianta arbustorum

	Density (adults m-2)				**Population size**	
	Transformed		Derived		95% C.L.	
Area	Mean	S.E.	Mean	Area (m^2)	Lower	Upper
B1	0.318	0.0744	1.08	1353	877	2002
B2	0.273	0.0719	0.875	1353	667	1704
B3	0.307	0.0592	1.03	1189	856	1593
B4	0.0708	0.0410	0.177	1168	-	461
B5	0.306	0.0834	1.02	1186	707	1708
B6	0.274	0.0713	0.879	1558	814	1932
B7	0.145	0.0519	0.396	1783	253	1159
M	0.082	0.0377	0.208	3813	90	1472
T	0.035	0.0024	0.084	3259	-	648
TOTAL				16662	4260	12700

Cepaea hortensis

B1	0.081	0.0377	0.205	1353	18	538
B2	0.218	0.0486	0.652	1353	542	1221
B3	0.301	0.0847	1.00	1189	646	1731
B4	0.091	0.0426	0.233	1168	18	529
B5	0.260	0.0541	0.820	1186	639	1305
B6	0.345	0.0449	1.21	1558	1530	2249
B7	0.233	0.0542	0.710	1783	763	1768
M	0.215	0.0557	0.640	3813	1336	3548
T	0.018	0.0176	0.042	3259	-	420
TOTAL				16662	5490	12900

Analysis of variance between areas
(Log x+1 transformed data)

Arianta arbustorum: F = 2.76, d.f. = 7;128, **P =0.01**

Cepaea hortensis: F = 2.87, d.f. = 7;128, **P <0.01** likley to have been important during the winter predation period.

DISCUSSION

The results of this study show that in both years snails were eaten by song thrushes in two distinct predation periods. Similar results were obtained by Goodhart (1958) in a three year study of snail predation in an area of open woodland. However, there appears to be variation in this pattern of predation because in some cases it has been shown to be restricted to the winter (Richardson 1975) or summer (Williamson, Cameron and Carter 1987), whilst Davies and Snow (1965) and Cameron (1969a) found that although there were clear winter and summer peaks in predation snails were taken throughout the year.

It is widely accepted that predation is restricted to periods when alternative food is unavailable (Jones, Leith & Rawlings 1977). Goodhart (1958) has suggested that this is because snails are normally unpalatable to song thrushes. However, there is no direct evidence for this. Another plausible explanation is that the snails are ´unprofitable´ food items because of the costs incurred carrying the snail to the anvil and then breaking open the shell. If this is correct, then the thrushes could be expected to feed optimally (i.e. maximize their net energy intake rate (Krebs & Davies 1978)). Snails would then only be eaten when the absolute density of more profitable food items falls to a level at which selecting a snail contributes more to the overall rate of net energy intake than would ignoring it and continuing the search for more profitable food. It is well known that earthworms are important dietary items for the song thrush (Collinge 1924-27; Davies & Snow 1965) and their accessability to thrushes is affected by periods of hard frost and prolonged hot and dry weather (Evans & Guild 1947; Lockie 1955; Gerard 1967). My study has shown that such periods of extreme temperature were highly correlated with the levels of snail predation. Similar observations were made by Goodhart (1958) and Davies & Snow (1965) although they lacked detailed meterological data to confirm the relationship statistically. Davies and Snow found that increased snail predation coincided with periods of low earthworm availability in February and again in August. Thus, there is good evidence that snail predation is generally restricted to periods when earthworms are unavailable or unprofitable food items; that is, when soil temperature is very low and very high. Hot weather in the early summer and late autumn may not induce snail predation if other food sources such as caterpillars and fruit are available at these times.

There were significant differences in the morph ratios of adult *Cepaea hortensis* between seasons (Table 2.18). There are at least three plausible reasons for this. First, there may have be differential survival of the morphs between late winter and late summer (i.e. between the times of the surveys). Second, juvenile morph frequencies may have been different from those of the adults because of different selective pressures acting on the two age-groups, and thus the summer adult morph frequencies are affected by recruitment from the over-wintering juvenile snail population. Third, sampling efficiency of the morphs may have varied between winter and summer, either because of behavioural or visual differences of the morphs (or both). However, this last possibility seems unlikely, because care was taken to search thoroughly all levels of the vegetation and the upper soil layer in each survey quadrat. This study cannot distinguish between the first two explanations.

The differences between winter and summer *Cepaea hortensis* morph frequencies invalidate direct comparisons of winter and summer predation. Similarly, the comparisons by Goodhart (1965) and Cameron (1969a) of seasonal differences in morph predation by song thrushes, in which they both suggest that pink unbanded morphs are taken less in winter, may be misleading.

Comparisons of the frequencies of predated *Cepaea* with those available showed that in winter 1985, pink unbanded and five-banded morphs (without fusions) were eaten significantly less often than expected (Table 2.19), and thus were at a selective advantage. Five-banded morphs were also at a selective advantage in the summer, as were yellow unbanded morphs. Sheppard (1951) found that yellow unbanded morphs of *Cepaea nemoralis* were taken less often by thrushes in late spring than early spring and he interpreted this change as a consequence of the increase in new vegetation which changed the background colour from predominantly brown to predominantly green. Wolda (1963) and Carter (1968a) obtained similar results, although they found that the selective advantage of the yellow morph decreased later in the summer as the background became darker again. In my study the main summer predation period in both years occurred in July and no predation occured in April or May, the period studied Sheppard (1951). However, unlike Wolda´s and Carter´s studies there was no indication in my work that selection changed during the period of summer predation (Tables 2.12 and 2.14). My study also showed that in the summer both classes of morph with fused bands were at a selective disadvantage with respect to thrush predation. Thus, the assumption that morphs with fusions which do not include the upper three bands, are effectively unbanded with respect to thrush predation is not supported by these results.

These results can be explained on visual grounds, whereby yellow unbanded and five-banded morphs are assumed to be cryptic against predominantly green or ´striped´ backgrounds, whilst other morphs are conspicuous. We must bear in mind, however, that the visual world of the song thrush may be very different from our own. There may be differences in the perception of colour and tone, and differences in the scale and perspective of background components as seen from the hunting position of the thrush.

The summer predation results can also be explained on the basis of shell colour and its effect on internal body temperature. Dark shells absorb more solar radiation than light shells and thereby reach higher equilibrium temperatures when exposed to strong sunlight (Emberton & Bradbury 1963; Heath 1975). Thus dark shells may be restricted to the lower shaded areas of vegetation in hot conditions, and thus could be more prone to thrush predation than snails which climb beyond the reach of ground-feeding birds. Wolda (1965) found significant differences between morphs in their climbing behaviour, although the relationship between morph and behaviour was not consistent from population to population. In a later study Jones (1982) showed that unbanded snails do seem to differ in behaviour from banded morphs and spend more time exposed to sunlight. Alternatively, climbing might help snails regulate their temperature at times of excessive heat by escaping radiation from the hot ground surface (Jaremovic & Rollo 1978), in which case dark morphs would be expected to climb more often than light morphs because they are more prone to heat stress. However, this behaviour is unlikely to occur in overgrown habitats such as at Rogate where dense vegetation shields the ground from sunlight.

Lamotte (1951) suggested that song thrush predation in France was non-selective during the winter, because the snails are buried and therefore were not detected by visual cues. The results of my study do not support this view. Song thrushes were observed searching for snails during the winter and it was apparent that they did use visual cues to locate snails which were not completely buried, i.e. those that were only partially hidden by soil and vegetation. Thus the visual properties of the snails would have been important in affecting the probability of detection. My observations showed that song thrushes searched by slow and deliberate inspectiion of the ground in front of them. They did not systematically dig or probe with the bill, nor turn over leaf litter, both of which are common behaviours of the closely related blackbird (*Turdus merula*). Bill probing only appeared to occur when a snail had been located, because such behaviour always resulted in the capture of a snail. Secondly, this study showed that visual selection occurred, with pink unbanded morphs selected more often than expected and five-banded morphs selected less often.

At the start of this study, it was hoped that the effect of morph frequency on *Cepaea* selection could be investigated by the manipulation of the existing morph frequencies through the removal and addition of appropriate morphs. Winter predation was the major period of selection by song thrushes and therefore any experimental investigation of selection would have been best carried out in this period. Furthermore, the vegetation structure at this time of year would have made sampling of the live population easier than during the summer. Also, the snail population would have been lower and the proportion eaten. Consequently, the removal and addition of the snail morphs in the study area would have required fewer numbers than in a summer experiment. In such an experiment the snails would be added in the autumn in order to ensure thorough dispersal and natural hibernation behaviour.

It was intended to change the pink unbanded and five-banded morph frequencies to 20% and 60% respectively. However, from the initial mean morph frequencies over the two winters of 30% and 48%, and a total *Cepaea* population of 12900 (i.e. the upper 95% confidence limit for the population estimate from the 1985/86 winter survey), then 1200 pink unbanded snails would have had to have been removed and 2640 five-banded morphs added to the population. This scale of experiment was beyond my resources. Furthermore, the addition of snails would have involved the use of snails collected from another colony. Differences in behaviour between the immigrant and ´native´ snails could have been checked but could not be controlled for. It was decided to abandon any attempt to carry out such a large scale field experiment, and instead use live snails and captive song thrushes.

CHAPTER 3

SELECTION BY SONG THRUSHES FEEDING ON *CEPAEA HORTENSIS*

INTRODUCTION

Clarke (1962a) developed the earlier ideas of Poulton (1884); Fisher (1930) and Cain & Sheppard (1954), and suggested that predators could potentially maintain visual polymorphisms if they tend to feed disproportionately more on common forms of prey. Thus, this form of frequency-dependent selection, termed "apostatic selection" by Clarke and later "switching" by Murdoch (1969) (when refering to inter-specific selection) conveys a selective advantage to prey when they are rare. Apostatic selection has been demonstrated in many experiments using a variety of predators and artificial prey (Allen & Clarke 1968; Allen 1972, 1976; Manly, Miller and Cook 1972; Harvey, Birley & Blackstock 1974; Fullick & Greenwood 1979; Willis *et al.* 1980; Shelton 1986) or natural but non-polymorphic prey (Popham 1941, 1942; Maskell, Parkin & Vespoor 1977; Cornell & Pimentell 1978; Akre & Johnson 1979; Bergelson 1985). An experiment by Reid (1987) using dimorphic colonies of the mangrove snail (*Littoraria filosa*) provides the only field study based evidence of apostatic selection on natural polymorphic prey.

Clarke (1962a) originally suggested that apostatic selection might be a process that contributes to the maintenance of polymorphisms in *Cepaea*. Although he provided supporting indirect evidence, based upon the divergence of *Cepaea nemoralis* and *Cepaea hortensis* morphs in mixed colonies, the only direct evidence that song thrushes might behave in such a manner comes from two experimental studies. Harvey, Birley & Blackstock (1975) showed that song thrushes took an excess of familiar brown bread-stuffed *Cepaea nemoralis* and *Cepaea hortensis* shells from a dimorphic population of brown and yellow morphs after training on the brown morph. Similarly Allen, Raymond and Geburtig (1988) have recently shown that thrushes took an excess of familiar morphs in experiments using pastry-stuffed yellow unbanded and yellow five-banded morphs of *Cepaea hortensis*. However, although both studies demonstrated that song thrushes modified their behaviour in response to recent experience of one morph, this does not neccessarily indicate that apostatic selection would occur in a natural polymorphic situation. Apostatic selection on *Cepaea* by song thrushes thus remains to be demonstrated.

This experimental study aimed to test whether song thrushes predate in an apostatic manner when presented with an artificial dimorphic population of *Cepaea hortensis*.

METHODS

A series of dimorphic ´populations´ of yellow five-banded and yellow unbanded *Cepaea hortensis* were presented at two frequencies, to a series of captive song thrushes. The background was short grass. Uneaten snails were recovered from each population so that a new population could be used in each predation trial. The effect of frequency on the selection of morphs was investigated using the analytical technique of Manly (1973). The experiments were carried out between November 1986 and January 1987.

Aviary and snail arena

The experiments were carried out within a large (20 m long x 6.2 m wide x 3 m high) outdoor aviary (Plate 3.1) situated within the University of Southampton Botanic Gardens. The aviary is constructed from a rigid angled-steel framework covered with chicken wire. Access was from the end furthest from the snail arena, alongside which there is a permanent wooden hide. Observations of the thrushes were made from the hide with the aid of 10 x 40 binoculars. A 5 m section at the hide end of the aviary was covered with corrugated plastic roofing to provide shelter for the captive birds. A large open-fronted wooden box and bushes were also present to provide roosting cover.

The snail populations were presented to the thrushes within a 4 m x 3 m arena, bordered by a 150 mm high plywood wall (Plate 3.2). The snails were prevented from crawling over the wall and leaving the arena by a simple electrical barrier. Two 4 mm high copper strips were attached on the inside of the wall 5 mm from the top and separated from each other by 5 mm (Fig. 3.1). Each strip was connected to one pole of a 12 v car battery, so that any

Plate 3.1. The outdoor aviary used in the captive thrush experiments, (photographed during preliminary trials in December 1985).

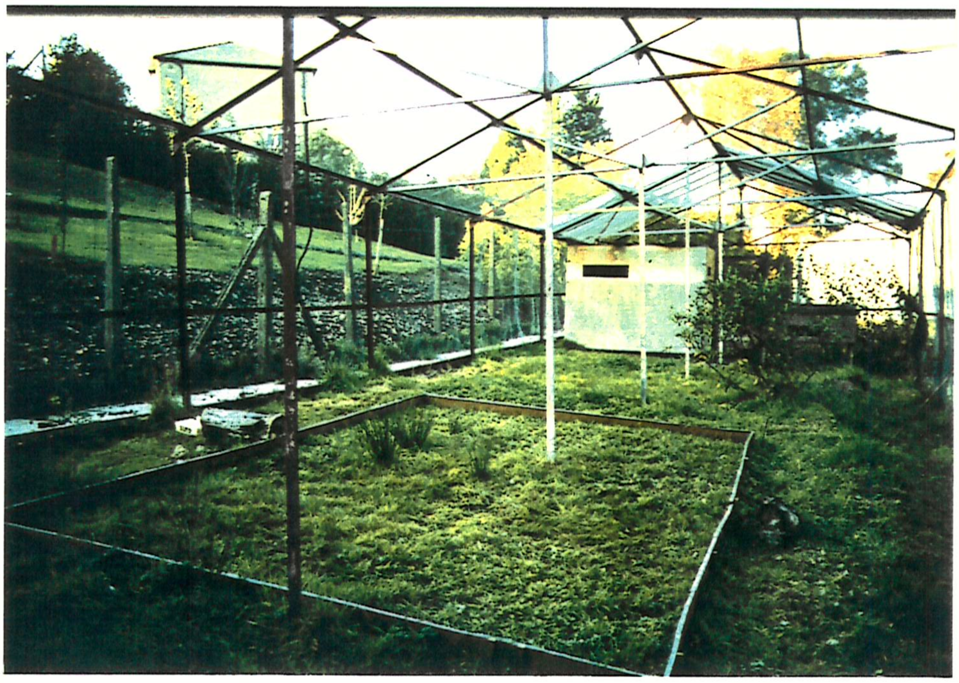


Plate 3.2. View of the snail arena and observation hide within the aviary. (Photographed December 1985).

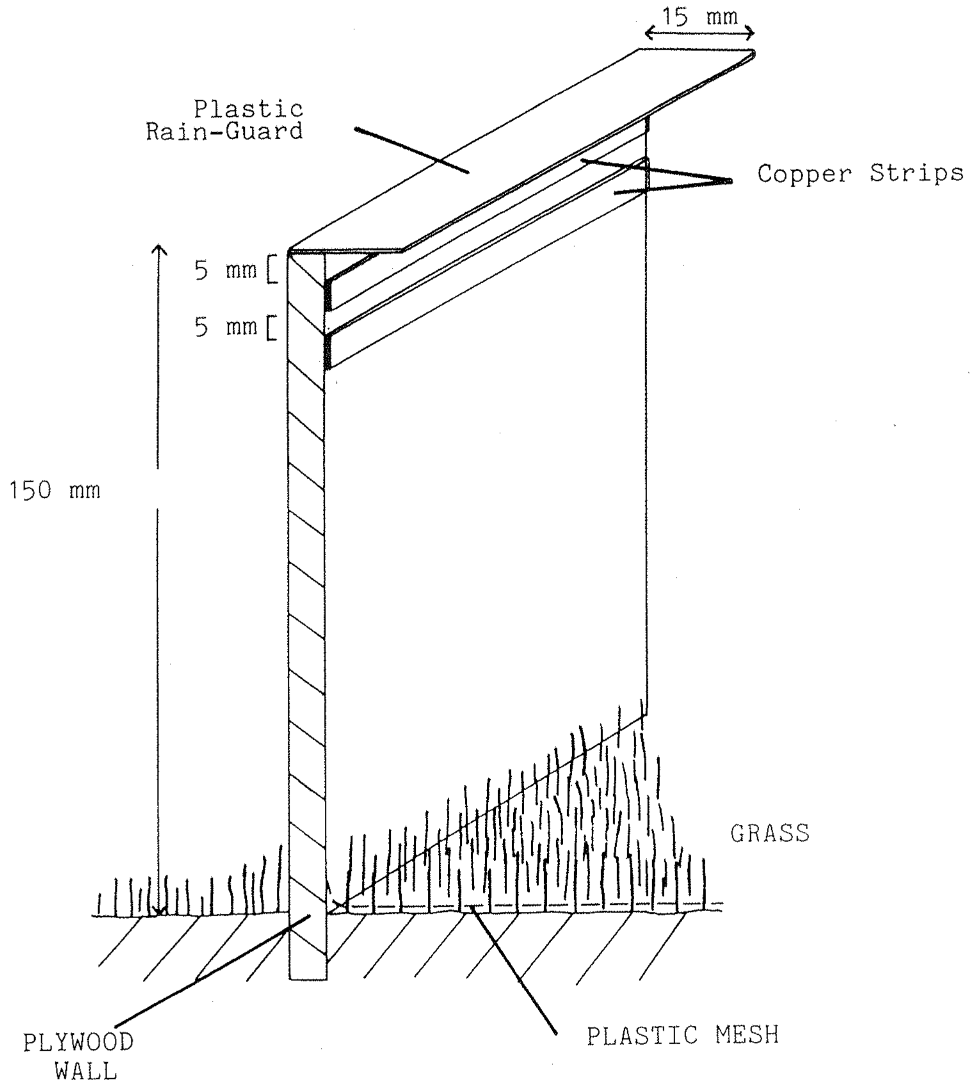


Figure 3.1. Diagramatic representation of a section of the arena wall.

connection made between the two copper strips would complete the electrical circuit. The battery was connected to opposite ends of the (14 m) copper strips so that a consistent circuit resistance and hence current was obtained irrespective of where a circuit was completed between the two strips. Thus snails attempting to cross the strips received an electric shock and preliminary experiments showed that they immediately dropped back into the arena. The barrier was found to be totally effective and did not appear to harm the snails. A 15 mm wide plastic strip was attached to the top edge of the wall to protect the copper strips from rain and the consequential risk of short circuiting.

The vegetation in the arena consisted of mixed lawn grasses, and creeping buttercup (*Ranunculus repens*). This was cut to 400 mm high with a pair of garden shears immediately before the start of the experiments. Preliminary trials were carried out in autumn 1985 with yellow unbanded and yellow mid-banded (00300) morphs of *Cepaea nemoralis*. However, the snails persistently buried themselves in the base of the vegetation and it was impossible to find them all at the of each trial. To overcome this, after cutting the vegetation in the spring (1986), green plastic netting (greenhouse shading material) was placed over the vegetation which then grew through the netting during the summer. The vegetation was then cut back to the required height in the autumn before the experiments were carried out. Three large flint rocks were placed alongside the arena to provide ´anvils´.

Cepaea hortensis collection and presentation

All the *Cepaea* used in this experiment were collected from a single colony along approximately 100 m of hedgerow and roadside verge (Ordnance Survey grid reference ST116749) below Hackpen Hill, on the Malborough Downs, Wiltshire, on 27 September 1986. Approximately 1000 adults were collected from the site. These were almost entirely yellow unbanded (Y 00000) and yellow five-banded (Y 12345). The snails were sorted according to morph and stored in paper lined cardboard boxes in a dark 5°C constant temperature room.

Four thrushes were used in this experiment and four predation trials were carried out for each. Thirty snails were used in each trial at frequencies of 9:1 or 1:9 yellow unbanded : yellow five-banded. The morph frequency presented to each thrush was the same for all trials. The frequencies used in the experiment were presented in a random order.

The snails were presented to the thrushes by haphazardly scattering the snails within the arena. This was always done at dusk, so that the snails could disperse and adopt hidden and natural positions in the vegetation during the night. Thus thrush predation did not start until the following morning at the earliest. Frequent observations were made from the hide during predation periods and the anvils were occasionally visted to establish the number of predated snails. When 15 snails had been eaten or broken the trial was stopped, and broken shell remains and rejected snails (i.e. snails picked up and taken to the anvil but not broken) were collected and recorded. The arena was then carefully searched with the aid of a grass-rake for the remaining snails, which were collected and recorded. Remaining and rejected snails were not re-used in later trials. Predation exceeded 15 snails on only two occasions. The data for these two trials were disregarded and the trials repeated. After each trial, the maximum aperture diameter of all intact and broken shells were measured (when possible) with vernier calipers. These measurements were used to check for size differences between morphs, and for differences between eaten, rejected and remaining snails. Measurements were not obtained for the first two trials and first trial with the first and second thrushes respectively.

In order to identify any remaining snails which had been overlooked after previous trials, all snails in each trial batch were marked with a unique combination of 1 - 5 0.8 mm holes drilled immediately behind the lip.

Thrush capture and welfare

Immediately before each set of trials a song thrush was caught by mist net (under licence from the British Trust for Ornithology) at either of two sites. Four thrushes were caught in an area of scrub alongside Southampton Docks and one in an urban garden in Southampton. Each bird was ringed (with a BTO metal ring), aged according to tail shape and the pattern of moult in the greater wing couverts (Svennson 1984) and weighed before release in the aviary (Table 3.1). Although the origin of the birds was unknown, it is likely they were migrants; part of the usual large influx of over-wintering thrushes into the area.

In addition to snails, live mealworms (*Tenebrio* larvae) and "softbill" (a commercial food for insectivorous birds) were provided *ad libatum* as supplementary food. After capture each thrush was left undisturbed for 24 hours before the presentation of the snails and the start of the first trial. This allowed the birds to adjust to their surroundings. In several cases the thrushes ignored or ate very few snails in the initial few days of captivity. Two birds were released without any trials completed, because they were not feeding satisfactorily. The last thrush completed three trials, after which it ceased feeding on snails and was therefore released. Each bird was reweighed before release in order to assess the effect of captivity on overall body condition. The birds were retained in captivity under a licence granted by the Nature Conservancy Council (Ref. SB:72:86).

RESULTS

Although it had been intended to test 6 thrushes for each frequency it became apparent early in the experiment that the thrushes were difficult to work with. Three individuals did not adjust to their surroundings readily and would not feed on the snails and one bird would not even take the supplementary food. Furthermore, the rate of snail predation was generally low, so that the trials took longer than expected to complete. Thus, the speed of the experiment was lower than anticipated and only four sets of trials were successfully completed by the end of January (the end of my Research Studentship).

Comparison of the thrushes´ weights at capture and before release showed that all of them lost weight over the period of captivity (Table 3.1). Thus, even when the thrushes were feeding intensively on snails and took supplementary food as well as other natural food in the aviary (e.g. earthworms) the birds showed a decrease in overall body condition. Although this may be partially attributable to stress-related factors, it also suggests that the snails had a low nutritional value.

Table 3.1. Details of song thrush captures and captivity.

Capture Date	Site	Age	Initial Weight (g)	Complete Trials	Captive Period	Release Weight (g)
20/11/86	Docks	1	?	4	8 days	67.5
28/11/86	Docks	1	80.5	4	8	64.5
12/12/86	Docks	1	78.5	0	5	60.5
6/1/87	Docks	1	88.0	4	4	72.0
20/1/87	Shirley	Ad	97.0	0	2	76.0
26/1/87	Docks	Ad	94.0	3	5	75.0

Age: 1 = 1st year bird, Ad = Adult

The mean number of each morph eaten was calculated for each thrush and used for the calculation of Manly's (1973) Beta selection coefficient. Confidence limits were also calculated, based upon the confidence limits of the mean numbers eaten. Table 3.2 summarises the predation by the four thrushes and presents the Beta estimates for each set of trials. In three out of the four sets of trials selection was apostatic. In the remaining trial (thrush 3) selection was neutral over all four trials (a Beta value of 45 is the coefficient expected in the absence of selection) However, examination of selection throughout the course of thrush 3's trials suggests that selection was initially anti-apostatic and became apostatic as the bird gained experience, although this trend was not statistically significant (regression analysis of individual Beta estimates against trial order; $y = 85.3 - 19.1x$, $t = -3.29$, d.f. = 2, $P < 0.1$). Thus, although the data suggests apostatic selection clearly more experiments are needed.

After each trial the unselected and rejected snails were recovered. However, after some trials some snails were not found, despite intensive searching. The most likely explanation for this was that the thrushes had carried the snails out of the arena but not to the anvils. This was actually observed on two occasions during observations of three trials (on birds 1 and 2) and appeared to be due to the thrushes searching for a suitable anvil and eventually abandoning the snail. Snails were also abandoned at the anvil (i.e. rejected) for no apparent reason, although these were usually recovered. Thus, the initial population size and morph frequencies could not be reliably established nor kept constant throughout the trials. However, it was clear that the thrushes generally restricted their snail searching to the arena (presumably after learning that this was the most profitable area), and therefore the 'lost' snails outside this area had a lower probability of detection than those left in the arena. In addition, the vegetation outside the arena was denser and longer, and this further reduced the probability of detection. Therefore, although it was possible to recalculate the presented morph frequencies on the basis of the missing snails, this was not done because it was unlikely that it would accurately represent the population being predated. Examination of the drill marks on the

Table 3.2. Manly's Beta selection coefficient estimates for captive song thrush predation of yellow unbanded and yellow five-banded morphs of *Cepaea hortensis*.

Thrush	Presented		Eaten*		Mean Eaten		Beta	Beta		Notes
/Trial	Y5	YU	Y5	YU	Y5	YU	(Y5)	95% C.L.		
1A	27	3	14	1						
B	27	3	14	1						
C	27	3	15	0						
D	27	3	15	0	14.5	0.5	**64.1**	46.2	90	2
2A	3	27	1	14						
B	3	27	1	14						
C	3	27	1	14						
D	3	27	1	14	1.0	14.0	**36.7**	–	–	
3A	3	27	3	12						1
B	3	27	3	12						1
C	3	27	1	14						
D	3	27	0	15	1.5	13.5	**45.0**	0.00	56.9	3
4A	27	3	15	0						
B	27	3	14	1						
C	27	3	14	1	14.3	0.67	**60.0**	36.3	90.0	2
D	27	3	7	0	(Trial incomplete - data not used)					

Y5 = Yellow five-banded morph, YU = Yellow unbanded.
Beta selection coefficients are arcsin transformed.
95% Confidence limits based upon t = 3.18 (n=4), t = 4.30 (n=3).
* Trials stopped when 15 prey eaten.

Notes

1. All rare prey were eaten - Beta calculated by adding 1 rare prey to total presented.
2. Confidence limits confined at complete predation of common prey.
3. Confidence limits confined at complete predation of rare prey.

shell remains of the eaten snails revealed that although snails remaining from previous trials were eaten in 5 of the 16 trials, this involved only 10 snails out of a total of 232 (ie. 4.3%). Thus, it is clear that there was a small but appreciable degree of error in the presented morph frequencies and therefore the Beta selection coefficients can only be regarded as approximate (except for the first thrush, where unrecovered snails were absent).

After each trial the aperture diameters of the presented snails were measured for both morphs and compared to check whether any size related selection could give rise to preferences for either morph. Also the aperture diameters of eaten, rejected and remaining morphs were compared to establish whether the thrushes were selecting for size. The results of these comparisons are presented in Table 3.3. There were no significant differences between the mean aperture diameters of yellow unbanded and yellow five-banded morphs, nor between eaten, rejected and remaining snails of these morphs.

DISCUSSION

This experiment attempted to simulate as closely as practically possible the natural predation of a dimorphic population of *Cepaea hortensis* in a grassland habitat by song thrushes, in order to investigate the effect of frequency on morph selection. The results suggested that song thrushes did select an excess of the common morph, but the effect was not statistically significant. This was in part due to the very small number of birds tested. Although further trials would be worthwhile there were problems with the methodology that suggest that an alternative experimental technique might be more productive. Firstly, the song thrushes would not always feed on the snails and for those that did, predation rates were often slow. Secondly, the birds clearly suffered a loss in condition over the period of captivity. Therefore, the experiments could not be prolonged to obtain more trials per bird and investigate longer term effects. On ethical grounds, the risk to the birds brings into question the justification of the experiments. Thirdly, despite the restrictions on snail dispersal and burrowing, some snails could not be recovered at the end of each trial. Hence it was not possible to hold constant the morph frequencies at the beggining

Table 3.3. Mean aperture diameters (mm) of the yellow unbanded and yellow five-banded *Cepaea hortensis* morphs used in the predation trials and comparison between selected, rejected and remaining snails.

Morph	Class	n	Mean	S.E.	Range
YU	All	192	9.11	0.0287	8.15 - 10.3
YU	S	100	9.12		
YU	RJ	27	9.09		
YU	RM	65	9.10		
Y5	All	155	9.15	0.030	8.22 - 10.1
Y5	S	84	9.14		
Y5	RJ	23	9.16		
Y5	RM	48	9.17		

Class: S = selected, RJ = rejected, RM = remaining.

Analysis of variance results (class nested within morph)

Source	d.f.	S.S.	M.S.	F	P
Morph	1	0.150	0.150	0.98	0.323
Class	4	0.060	0.015	0.10	0.983
Error	341	52.33	0.154		
Total	346	52.54			

of each trial and the selection estimates were therefore unreliable.

Clarke (1961) also used captive song thrushes in experiments with yellow unbanded and yellow five-banded morphs of *Cepaea hortensis* to test whether training biases for the familiar morph would occur after feeding on large numbers of that morph. No training bias was found. Clarke suggested that the absence of a training bias was due to the birds being too familiar with the aviary and experimental set up, which caused them to feed non-selectively. This led to the abandonment of captive bird experiments and the adoption of experiments with free-ranging predators and artificial prey. There is now a wealth of information based upon this methodology, demonstrating apostatic selection, and the effects of prey density, palatability and degree of crypsis on the magnitude and direction of selection (see Allen (1988) for review). Despite the problems encountered in this experiment there is clearly a need for studies investigating selection of natural populations of prey by real predators. One such method could involve establishing populations of prey in the vicinity of wild predators, as done by Arnold (unpublished results cited by Allen (1988)) with *Cepaea nemoralis* and song thrushes. Although his results were not conclusive, he did demonstrate the value of the technique. Alternatively, the perturbation of existing morph frequencies in populations of prey can be used to test for apostatic selection, as successfully carried out by Reid (1987) on a species of mangrove snail (*Littoraria filosa*). However, investigations of the underlying behaviour behind apostatic selection necessitates detailed behavioural observations and to enable this the use of captive predators is usually required. Although captive song thrushes feeding on live *Cepaea* are not ideal, other predator-prey systems might be more productive.

CHAPTER 4

SELECTION BY SHORE CRABS FEEDING ON *LITTORINA MARIAE*

INTRODUCTION

As we have seen (chapter 1) there are now several lines of evidence that indicate that morphs of *Littorina* and *Littoraria* are subject to visual selection by predators.

One important class of predators on these marine molluscs is crabs (Reimchen 1974, 1982; Heller 1975b, 1976 Petit 1975; Smith 1975; Raffaelli 1978a; Reid 1984, 1987). Since colour vision has been demonstrated in some crabs (Buddenbrock & Friedrich 1933; Horridge 1967; Hyatt 1975 and Bursey 1984) they have the potential to exert visual and frequency-dependent selection on mollusc colour morphs and may contribute to the maintenance of these polymorphisms. Although Reid (1987) suggested that crabs may have been responsible for the frequency-dependent selection observed in field experiments on *Littoraria* at present there is no direct evidence that crabs either exert visual or apostatic selection.

This experimental study aimed to test whether shore crabs (*Carcinus maenas*) predate in a visually selective and/or apostatic manner, when presented with a dimorphic population of *Littorina mariae*; a species known to be eaten by *Carcinus* (Reimchen 1974, 1982; Heller 1975b, 1976; Petit 1975; Smith 1975; Raffaelli 1978a) and probably subject to visual selection (Reimchen 1974).

METHODS

A series of dimorphic populations of yellow and dark reticulated morphs of *Littorina mariae* were presented on a dark stone chipping background, against which the dark morphs appeared highly cryptic (see Plate 4.1), to a series of shore crabs (*Carcinus maenas*) housed separately in large tanks. Each crab was presented with 20 snails in just one of 9 possible morph frequencies (0.05, 0.1, 0.2, 0.35, 0.5, 0.65, 0.8, 0.9, 0.95). As in the previous experiment the effect of frequency on the selection of morphs was investigated using the analytical

Plate 4.1. An aquarium tank used in the crab predation trials.

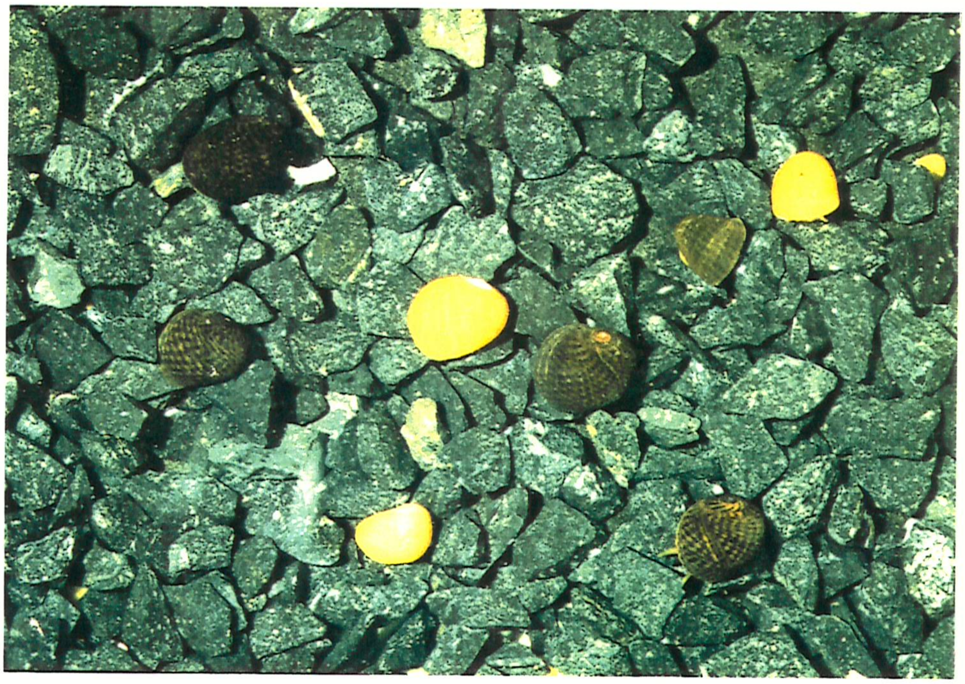


Plate 4.2. Dark reticulated and yellow (citrina) morphs of *Littorina mariae* on the dark stone chipping background.

technique of Manly (1973). The experiments were carried out between October 1986 and January 1987.

Aquaria tanks

The experiments were carried out in five white china tanks (150 mm deep x 540 mm long x 385 mm wide), connected to a large circulating seawater aquarium. The aquarium was housed inside a 5^0 C constant temperature room with a fixed 18 h daylight period. The water in each tank was constantly renewed at approximately 2 litres min^{-1} and kept at a fixed depth of 95 mm with an overflow pipe, thus giving a volume of 19.75 litres. The floor of each tank was covered with a 15 mm layer of dark grey/black stone chippings (5 - 10 mm maximum diameter), except for the outer 30 - 40 mm margin and the area around the overflow pipe, which was covered with a 15 mm layer of medium-coarse sand (see Fig. 4.1 and Plate 4.2). The sand was used as a barrier to the *Littorina* (as used by Reimchen 1979), in order to prevent them climbing the tank walls and overflow pipe and becoming inaccesible to the crab. The tank was covered with plastic netting and secured by ´velcro´ attachments in order to restrain the crabs and prevent any snails from escaping.

Collection of *Littorina* and method of presentation

The *Littorina* were collected from Bembridge Ledges on the Isle of Wight, (Ordanance Survey Grid Reference SZ658880) on several occasions between 1 October 1986 and 15 January 1987. All collections were made at low tide from the same 200 m x 10 m stretch of rock ledges immediately above the low spring tide water mark. Although exposed to heavy seas from the east the ledges are sheltered from the prevailing south westerly winds. Initially the snails were at high densities (in excess of 100 m^{-2}) on the abundant fronds of *Fucus serratus* and (the less common) *Fucus vesiculosus*, and amongst the rock crevices. However, the *Littorina* density fell to less than 10 m^{-2} after late November, probably as a result of a severe storm at this time, which also removed much of the *Fucus* cover.

After collection the snails were kept in the aquarium room but in two 10-litre tanks separate from the main aquarium water

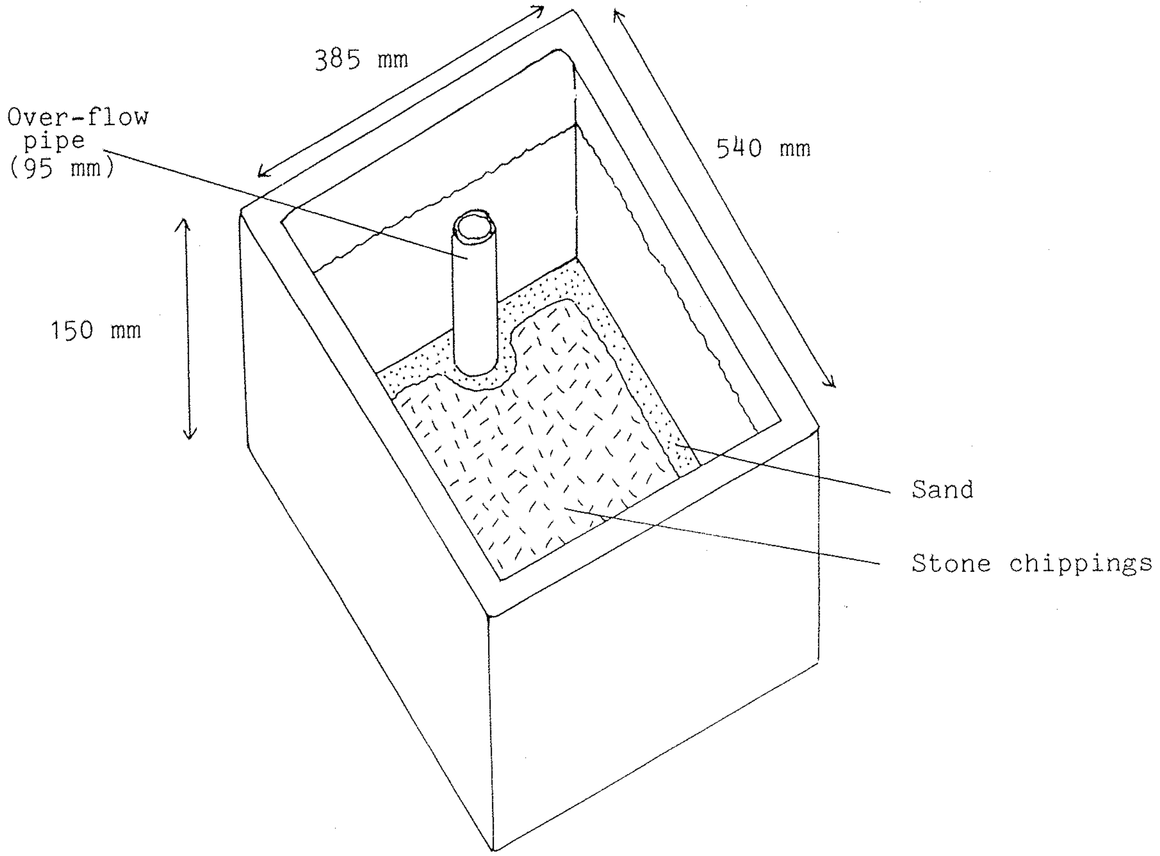


Fig. 4.1. Diagram of an aquarium tank used in the shore crab predation experiments.

system. Air was supplied to each tank by two air-stones connected to an electric pump. No food was provided for the snails.

Unwanted species were separated and the remaining *Littorina mariae* sorted according to size and morph. *Littorina obtusata* were identified according to the shell morphology criteria of Sacchi & Rastelli (1966) and Goodwin & Fish (1977). However, only juvenile *Littorina obtusata* occurred within the size category presented to the crabs, and these were easily separable from adult *Littorina mariae*. Only adult snails between 6 - 9 mm width were used in the experiment. The two commonest morphs were ´citrina´ (yellow) and dark reticulated, and these were used to form the dimorphic ´populations´.

Size has been demonstrated to affect the vulnerability of *Littorina* to crab predation (Reimchen 1974, 1982) ; Elner & Raffaelli 1980) and this could potentially affect morph selection. Therefore, for each morph a random sample of 30 snails was taken from the first batch of collected snails and measurements were made of shell width, height and aperture diameter (according to Goodwin & Fish 1977), and shell weight (after removal of the body). Ratios of shell width:height and width:weight were also calculated. Morphological parameters were analysed in order to establish whether there were differences between the yellow and dark morphs.

The required number of each morph was randomly taken from the experimental population before each trial. Only snails that were obviously alive and active were used. These were presented to the crabs by ´randomly´ sprinkling onto the stone chipping background. Trials were carried out with five crabs (in separate tanks) at a time. Frequent observations were made to establish the number of snails that had been eaten by each crab, each trial was stopped when 8 snails had been. If a trial was not complete by the end of the working day the remaining snails were recovered, stored separately overnight and replaced the following morning. If a trial was not complete after three days, the trial was abandoned and the crab replaced. Each crab carried out five trials unless a trial was not completed. Snails remaining intact at the end of each trial were discarded.

It had been intended to carry out three replicate sets of trials (i.e. with three crabs) for each frequency, over the course of the experiment. However, because of to the low predation rates of some crabs, the difficulty in obtaining *Littorina* after the population crash and the limited time, only 13 sets of trials were carried out. In three of these, the entire set of five trials were completed. Six crabs failed to complete their first trial over the initial three day predation period and these crabs were discarded (they are not mentioned in Table 4.2).

Collection and captivity of *Carcinus*

Crabs were collected from a tidal section of the River Itchin in Southampton (Ordnance Survey Grid Reference SU438131) using a fish baited crab pot. the crabs that were used in the experiments were all healthy (i.e. those with complete chelaea and legs and no obvious signs of parasite infestation) and had a carapace diameter of over 50 mm. No species of *Littorina* were present at the crab capture site. After capture the crabs were kept in large holding tanks within the circulating sea-water system of the aquarium for at least 5 weeks before use in predation trials. This eliminated their rythmic behaviour patterns. Chopped ox heart and whitebait were provided regularly during this acclimatization period, but was witheld in the 3 days before the trials. No food other than *Littorina* was provided during the trials.

Remote video recordings were made of two trials in order to observe the searching behaviour of the crabs.

RESULTS

The comparisons of morph shell structure showed that although yellow morphs tended to be larger and proportionally heavier, there were no significant differences between the colour morphs with respect to dimensions, weight or weight:size ratio (Table 4.1).

The results from the predation trials are shown in Table 4.2. In most cases the crabs did not complete their intended five trials, because at some stage they failed to eat 8 snails within the designated 3 day trial period. Predation rates were generally

Table 4.1. Between morph comparison of *Littorina mariae* experimental population shell dimensions.

Parameter	Mean Yellow	Dark	Mean Square	F	P
Width (mm)	8.05	7.92	0.242	0.488	0.488
Height (mm)	7.55	7.49	0.066	0.152	0.698
Aperture (mm)	7.02	6.93	0.121	0.311	0.579
Weight (gms)	0.202	0.185	0.0045	1.73	0.194
Wd/Ht	1.07	1.06	0.0007	0.450	0.505
Wd/Wt	41.9	45.2	165	2.00	0.162

n = 30 for yellow and dark reticulated morphs.
d.f. = 1,58

Table 4.2. Manly's Beta selection coefficient estimates for *Carcinus maenas* predation of yellow and dark reticulated morphs of *Littorina mariae*.

Crab	Trials	Presented		Eaten		Mean Eaten		Beta
		D	Y	D	Y	D	Y	(D)
11	3	19	1	23	1	7.67	0.333	48.5
15	2	19	1	16	0	8	0	90.0
10	3	18	2	24	0	8	0	90.0
13	1	18	2	6	2	6	2	31.3*
16	4	16	4	26	6	6.5	1.5	46.5
14	4	13	7	24	8	6	2	53.6
17	1	10	10	5	3	5	3	54.3
7	1	10	10	5	3	5	3	54.3
18	2	10	10	9	7	4.5	3.5	49.7
12	4	7	13	12	20	3	5	47.0
3	5	7	13	11	29	2.2	5.8	38.6
2	5	2	18	6	34	1.2	6.8	54.3
6	5	1	19	2	38	0.4	7.6	45.0

Trials = Total number of completed trials.
Y = Yellow morph ; D = Dark reticulated morph.
Eaten = Total of all trials (each trial was stopped when 8 prey eaten).
Beta = Manly's Beta selection coefficient for the Dark morph (arcsine transformed).
* Beta calculated by adding 1 to the number of rare prey presented.

low and variable. Therefore, the the overall speed of the experiment was lower than anticipated. Consequently, fewer crabs, and on average fewer trials per crab were carried out than intended. Thus the data set is incomplete. Furthermore, where crabs did only one trial, the Beta selection coefficient estimates are prone to bias, particularly at extreme prey frequencies. However, regression analysis of the Beta estimates against the frequency of dark prey clearly shows that slope of the regression line was not significantly different from zero and therefore there was no indication of frequency-dependent selection (Figure 4.2).

The mean Beta value with respect to the dark morph was 54.1 (S.E. = 4.80) and therefore suggested a preference for this morph. However, this value was not significantly different from 45, the value expected in the absence of selection ($t = 1.90$, d.f. = 12, $P = 0.0822$). Therefore the result shows that there was no frequency-independent selection for either morph. Thus, it seems unlikely that the crabs were using visual cues to locate their prey, because on this basis (assuming that our perception of the degree of crypsis of the morphs is similar to that of the crabs) we would expect a preference for the yellow, conspicuous morph. Clearly this was not the case.

DISCUSSION

The rate of predation was lower than expected in this experiment and six crabs failed to complete any trials. This was most likley a result of the resistance of adult *Littorina* to crab predation through the strength of their shells. The ability of *Carcinus maenas* to break *Littorina* shells has been shown to be related to shell size (Reimchen 1974, 1982; Elner & Raffaelli 1980). Furthermore, in laboratory experiments, only 28.0% - 34.7% of 6-8 mm *Littorina mariae* were consumed by six 40 - 60 mm (carapace width) *Carcinus maenas* (Reimchen 1982). These size categories correspond closely to those used in this experiment, although in my study the crab size range was 50 - 60 mm. Thus, predation was restricted by the inability of the crabs to break open the snail shells. Although it would have been possible to overcome this problem by presenting a smaller size class of *Littorina*, this was not practical, because small *Littorina* were at substantially lower densities than those used at the collecting

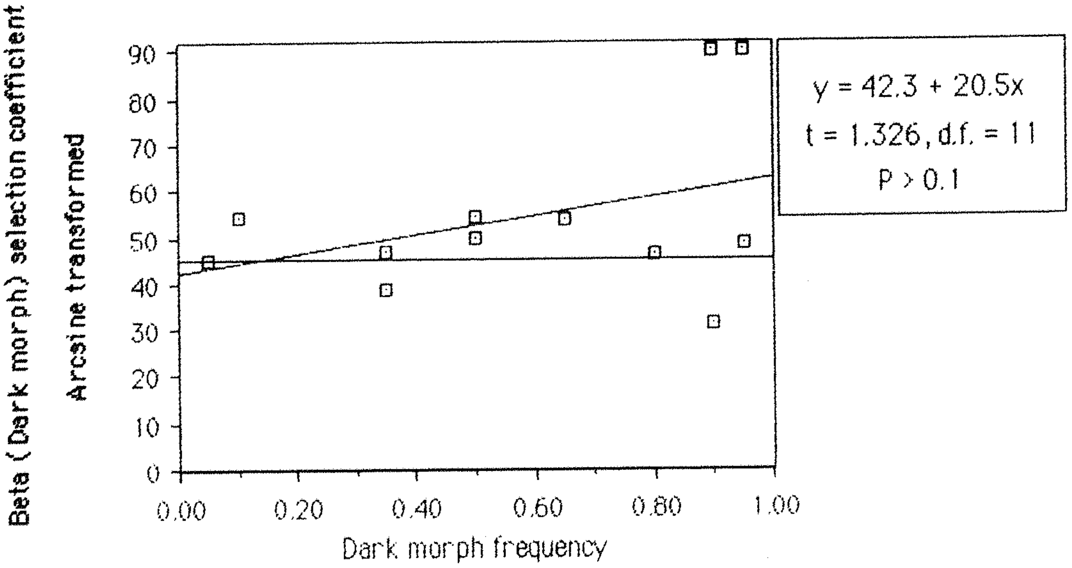


Fig. 4.2. Selection against the dark morph in relation to frequency. The horizontal line indicates the relationship expected in the absence of selection.

site. Larger *Carcinus* could perhaps have been used, but crabs larger than 60 mm were not trapped at the estuary catching site. These results agree with the conclusion of Reimchen (1982) that crab predation is likely to be most important at the juvenile stage of *Littorina mariae.*

This experiment aimed to test whether shore crabs would exert visual and apostatic selection on a dimorphic population of *Littorina mariae*. Although the sample sizes were small for some frequency combinations visual selection was clearly absent. Therefore, this does not support the suggestion by Heller (1975b) that *Carcinus maenas* may be a predator that contributes to the visual selection which has been observed in populations of the closely related *Littorina saxatilis*. However, in order to consider the generality of this result it is necessary to consider how the experimental system differed from natural predator and prey situations. First, the trials were carried out under artificial light and in a non-tidal environment. Crabs normally show rythmic peaks in activity that coincide with darkness and high tide (Crothers 1968). Second, the *Littorina* were presented on an unnatural substrate with an atypical background colouration. However, it is difficult to envisage how these differences from a natural situation could eradicate visual selection if searching by visual cues is a normal component of crab searching behaviour. Perhaps, crabs are adapted to searching in low light levels and therefore the bright illumination in these experiments interfered with their visual searching behaviour, but it seems more likely that the use of visual cues would be promoted by increased light.

Carcinus are known to use tactile and chemical cues when searching for prey (Crothers 1968). Crabs appear to make haphazard searching movements with their legs and respond instantly when a food item is touched, through information collected from chemo-receptors located at the tips of the crabs appendages. Crabs are also thought to be able to detect the presence of food in the vicinity with chemo-receptors on the antennae (Crothers 1968). Despite the lack of evidence indicating that visual cues are not used, *Carcinus* has been frequently dismissed as a non-visual hunter (e.g. Elner & Hughes 1978). From this study observations of the foraging behaviour of crabs and analysis of the video recordings taken for two trials indicated that in these trials the crabs appeared to search for their prey primarily by tactile means, as described above. In natural populations of *Littorina* many snails will be attached to fronds of Fucoid seaweed as well as the rock substratum. It is unlikely that crabs large enough to feed on *Littorina* will climb *Fucus* fronds, in which case snails on the seaweed would not be detectable by tactile means. Although it is possible that crabs detect prey by visual cues, it is probable that the *Fucus* population of *Littorina* generally avoids crab predation. Therefore, this experiment and the previous studies suggest that visual selection is not exerted on populations of *Littorina* through predation by *Carcinus maenas*.

CHAPTER 5

APOSTATIC SELECTION BY HUMANS SEARCHING FOR COMPUTER GENERATED IMAGES ON A COLOUR MONITOR.

INTRODUCTION

Frequency-dependent selection by predators has been demonstrated in several studies using artificial prey (eg. Allen and Clarke 1968; Allen 1972, 1974, 1976; Manly, Miller and Cook 1972; Fullick and Greenwood 1979; Raymond 1984) and natural prey (Den Boer 1971; Maskell, Parkin and Vespoor 1977; Cornell and Pimentell 1978; Akre and Johnson 1979; Bergelson 1985). However, very little information is available on the behavioural basis of apostatic selection. Although Clarke (1962a) suggested that the development of search images (Tinbergen 1960) is the primary cause of apostatic selection, there is only circumstantial evidence to link the two phenomena. Additionally it is now clear that a wide range of behaviours can in theory give rise to frequency-dependent selection by predators (Murdoch, Avery and Smythe 1975; Greenwood 1984).

The absence of data on this subject may result in part from the difficulty of combining experimental tests for apostatic selection with accurate and continual behavioural observation. Selection experiments are also very time-consuming and thus rarely provide sufficient replicates for detailed investigations of the behavioural mechanisms that may cause apostatic selection. These problems were overcome in this study by using a computer to generate the prey as images on a visual display unit (VDU), control and monitor the experiment, and by using humans as predators. The computer-controlled technique has the advantage of giving the experimenter considerable control over important variables (e.g. ensuring consistent exploitation), as well as providing a means for automatic and accurate recording of the data. The use of humans avoided the problems associated with capturing and housing real predators and training them to respond to prey images (e.g. Pietrewicz and Kamil 1979). Similar approaches in which humans have been used to test models were used by Holling (1959) in his development of the Type 2 fuctional response curve ("Holling´s Disc Equation") and by Gendron and

Staddon (1984) in an examination of the effects of search rate on the detection of cryptic prey images. Thus, despite the obvious pitfalls´ humans can be useful experimental subjects in the early stages of the development of models of behaviour.

The experiments (1a, 1b and 2) described in this chapter had the following aims: (1) to test whether humans select in a frequency-dependent manner when searching for dimorphic ´prey´; (2) to investigate the behavioural basis of any observed selection; (3) to establish the effects of prey depletion, density and experience on selection. Experiments 1a and 1b have been published (Tucker & Allen 1988).

METHODS

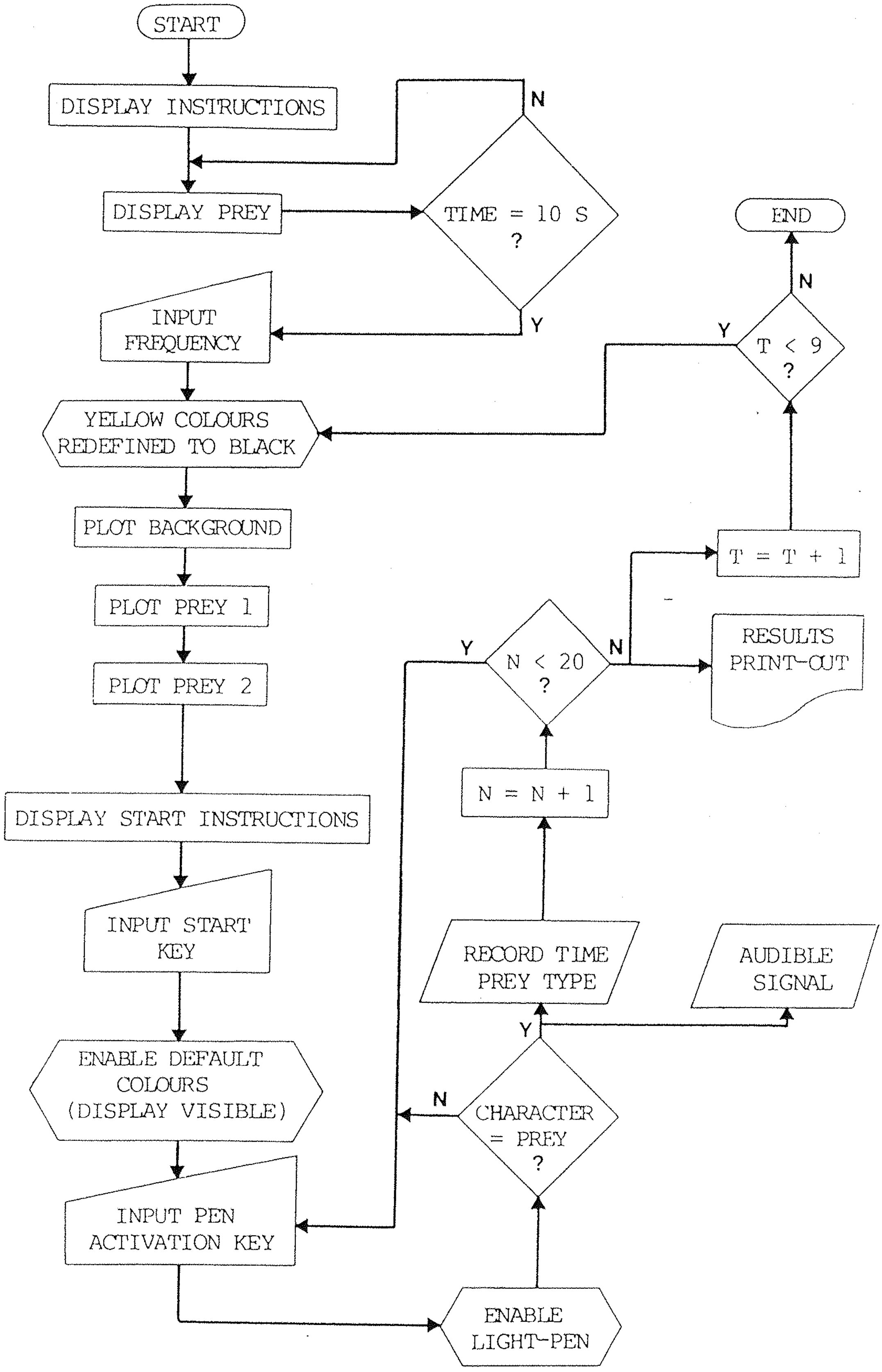
Experiment 1a

A series of dimorphic ´prey populations´ represented by computer-simulated images were presented on a VDU screen, against a background upon which they were cryptic, to a series of naive human subjects (´predators´). At the start of each trial each subject was presented with 40 prey, of two types, at one of seven frequencies. The subject then simulated predation by eliminating prey as fast as possible until the trial was automatically stopped when half the prey had been selected. A light-pen was used to remove prey from the screen.

The computer program.

The program was written in BBC Basic and used on a BBC Model B (32 K) micro-computer linked to a C ub Microvitec colour monitor. The program is listed in Appendix 1 and summarized in the form of a flow chart in Fig. 5.1. On the VDU the two prey types consisted of user defined characters in the form of patterns of yellow pixels (dots) in an 8 x 8 pixel matrix (7.2 mm^2), either in the shape of an open circle (prey 1) or an upper case letter ´T´ (prey 2). The background consisted of 800 characters also made up of a predetermined random pattern of yellow pixels (within an 8 x 8 matrix), which were randomly distributed over the dark screen. Each prey type was combined with a fixed set of pixels similar to the elements of each background character, in order to give the

Fig. 5.1. Simplified flow diagram of computer program used in experiments 1 and 2.



appearance that the prey were superimposed on the background, thereby concealing their presence. Fig. 5.2 shows the background pattern, prey 1 and 2 in isolation and combined with background elements. On the screen, the prey and background were displayed within a window 21.5 cm. wide by 15.5 cm. high, giving an effective density of 1200 prey m-2 in screen Mode 1 (see Fig. 5.3 for examples).

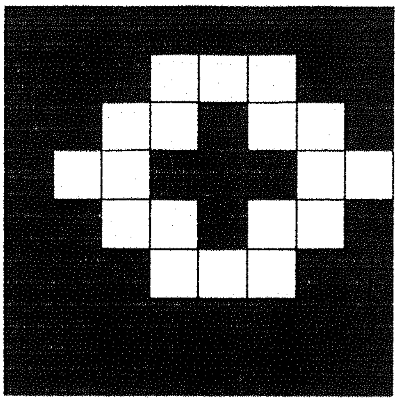
Whilst the background and prey were being generated by the computer all elements were the same colour as the screen and thus not detectable to the subject. After 13 s the distribution of prey and background was complete and the computer prompted the subject to press a defined key to start the trial. When commanded the computer redefined the prey and background characters to yellow making the display visible and thus enabled the subject to start eliminating the prey.

Prey were eliminated by placing the light pen over a prey item and pressing the ´Z´ key simultaneously. The computer then checked the appropriate character. If a prey item was detected the computer removed the character, emmitted a short ´bleep´ (to confirm the subjects correct identification of the prey) recorded the prey type selected, the time since the start of the trial and since the last item was detected. These data were printed out automatically when the program terminated the trial as soon as half the prey (20) had been selected.

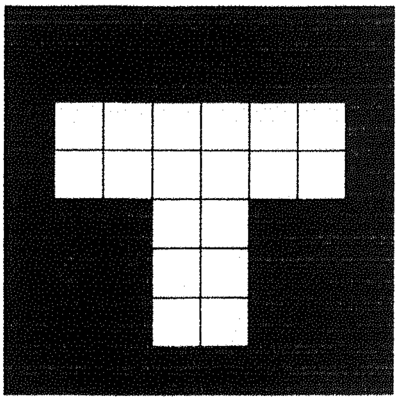
The VDU display was always set to maximum brightness to maximize and standardize the efficiency of the light pen.

Experimental procedure.

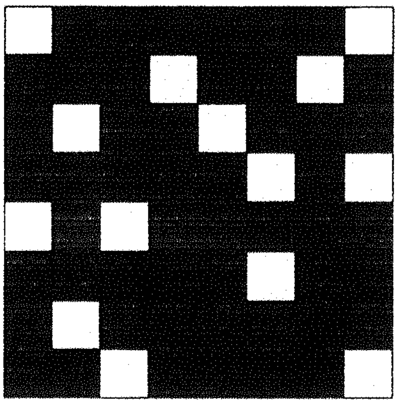
The subjects were 70 volunteers (33 female, 37 male) from the staff and students at the Medical and Biological Sciences Building, at the University of Southampton. Care was taken to ensure that each subject had no prior knowledge of the purpose of the experiment. Each subject was tested with prey at a single frequency of either 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, or 0.95 with respect to prey 1. The initial ´population´ size was 40 and prey were not replaced when selected.



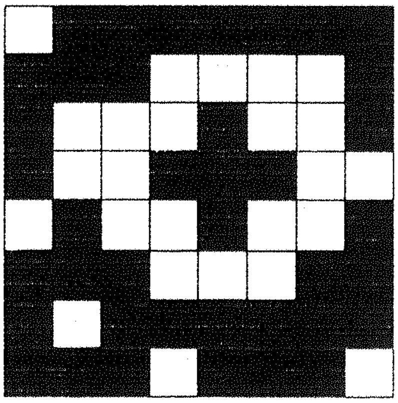
Prey 1



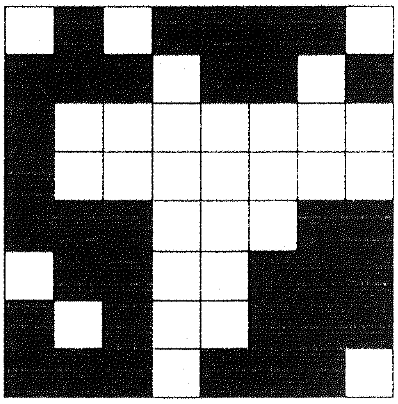
Prey 2



Background

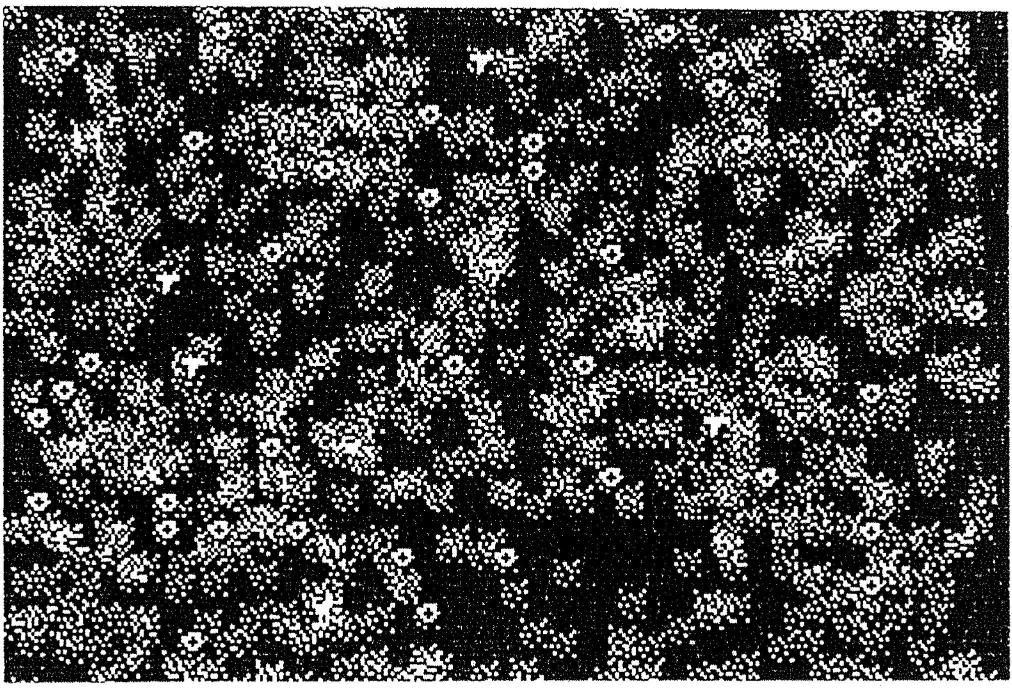


Prey 1 + Background

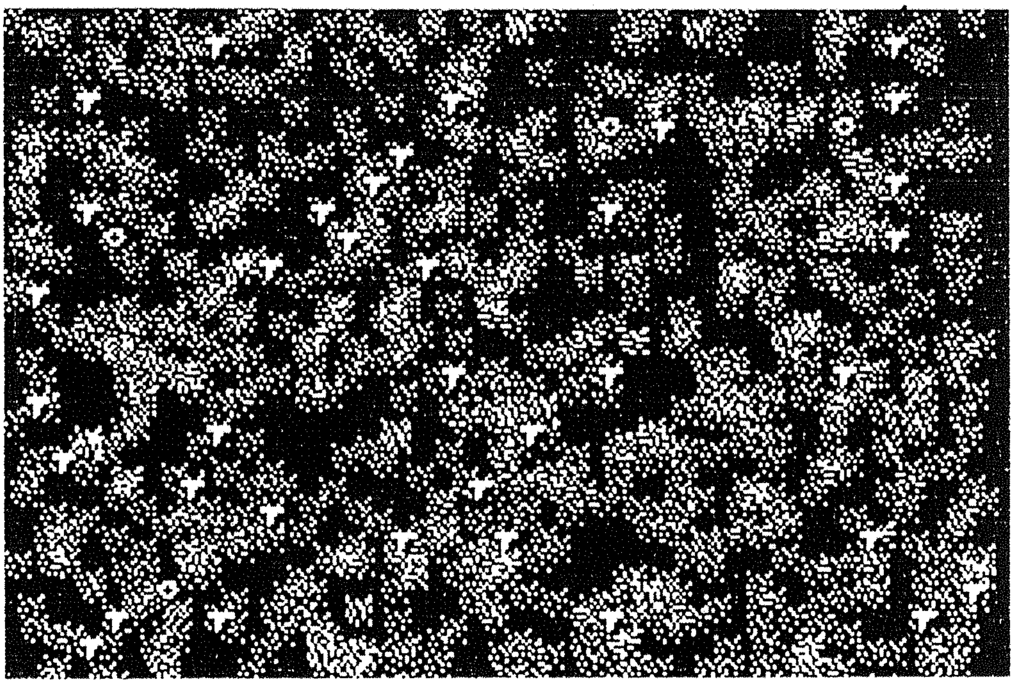


Prey 2 + Background

Fig. 5.2. Prey and background patterns used in experiments 1 and 2. These are user defined characters, each consisting of a 8 x 8 pixel matrix.



a)



b)

Fig. 5.3. Screen-dump printouts of typical backgrounds with 40 prey. (a) Frequency of prey 1 (circles) = 0.9, frequency of prey 2 (T-shapes) = 0.1. (b) Frequency of prey 1 = 0.1, frequency of prey 2 = 0.9.

Before the start of the first trial for a given subject the program displayed a set of written instructions stating that "an arena will be displayed on the screen consisting of a yellow background with scattered ′prey′ of the same colour. These prey items are represented by two different shapes." The subject was also instructed that "the task is to locate and delete either prey using the light pen as fast as possible." The use of the keyboard and light-pen was also described in the instructions. To counteract the possible effects of novelty (cf. Lawrence and Allen, 1983) the subject was then shown an example of each prey simultaneously displayed against a blank (dark) screen for 10 s. Prey frequency was entered into the program by the investigator using a code number and was therefore unknown to the subject. Each of ten subjects for each frequency performed nine trials, the first of which was for familiarization with the use of the keyboard and light-pen, and the data were disregarded in subsequent analysis. Thus for each frequency the subjects selected a total of 1600 prey.

After completion of their trials the subjects were asked whether they had knowledge of apostatic selection or switching behaviour. If they did, their trial results were disregarded in order to avoid potential bias. This was only necessary in two cases.

Analysis.

The analytical technique of Manly (1973) was used to test selection. For each subject the selection coefficient Beta (B) was calculated with respect to selection of prey type 1, from the mean number of each prey type remaining in the eight trials. The use of means avoided possible bias and inflated variance when subjects did not select any rare prey in a trial. Frequency-dependence was then tested by regression of arcsin transformed values of Manly′s Beta selection coefficient on the frequency of prey 1. A value of B of 45 indicates no selection; a value above 45 indicates selection against prey 1 , and below 45 selection against prey 2. A statistically significant slope suggests frequency-dependent selection and its intercept with the point where the prey are presented in equal frequencies gives an estimate of the frequency-independent preference for prey 1.

Experiment 1b

The experiment was carried out as described above with the following exceptions. Firstly, the yellow prey were presented against red background characters distributed over the dark screen and thus appeared conspicuous. However, a limitation of the computer hardware was that the background pixels accompanying each 8x8 user-defined prey character were unavoidably the same colour as the prey. Thus on the red and dark background the yellow prey were each immediately surrounded by a few yellow pixels. The alternative, of placing each prey in an area of blank screen, would have made both prey types more conspicuous irrespective of the background. In addition, the light pen recognized a prey item on the basis of all the pixels within the defined character; the removal of pixels in the immediate background could have thus significantly altered the 'handling' properties of the prey.

Secondly, only seven subjects were used for each frequency as it was found that this was sufficient to restrict the standard error of the selection coefficients to within 10% of the estimated mean. Therefore 49 volunteers (25 female, 24 male) were used, none of whom had taken part in the previous experiment.

Experiment 2

The aim of this experiment was to establish the effect of prey density on the frequency-dependent and frequency-independent components of selection. Two sets of trials were carried out using the same methods as Experiment 1a (with cryptic prey). In the first set, the initial frequency of prey 1 was 0.9 for each subject and each trial, whereas in the second set of trials the prey were always presented to the subjects in equal frequencies (P1 frequency = 0.5). However, the trials were carried out over a range of densities. For each frequency/density combination eight subjects were tested with prey at a single density of either 20, 40, 60, 80 or 100 prey per screen (21.5 x 15.5 cm) and at a single prey frequency. As in Experiment 1a and 1b each subject performed nine trials, although the first trial was for familiarization with the keyboard and light-pen, and therefore the data were disregarded in the subsequent analysis. In the 20 prey trials each

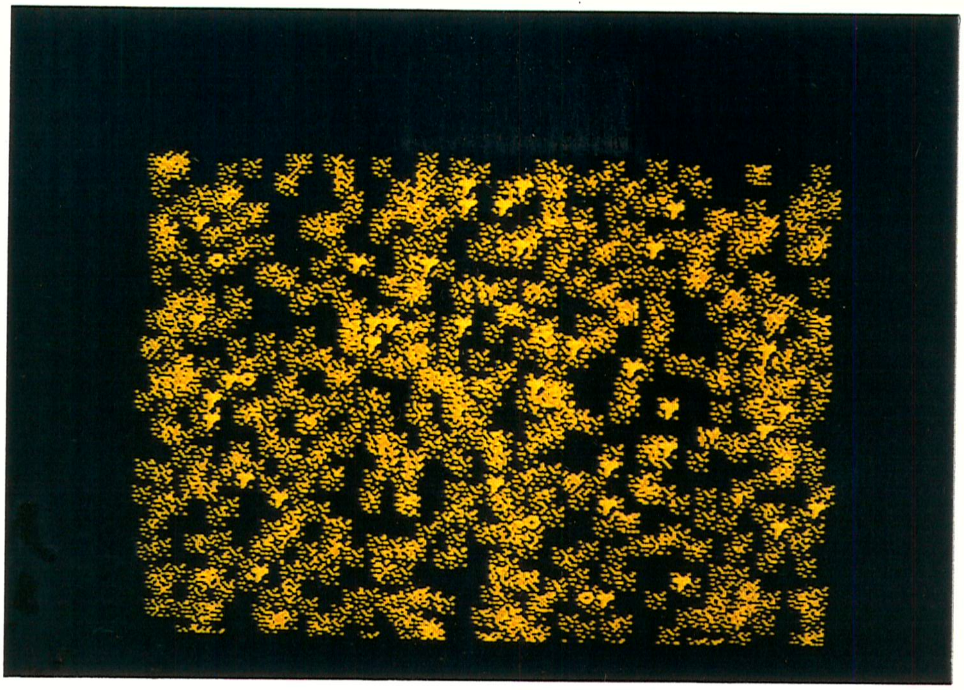


Plate 5.1. Typical background in Experiment 1a with cryptic prey. Frequency of Prey 1 (circles) = 0.1, frequency of Prey 2 = 0.9.

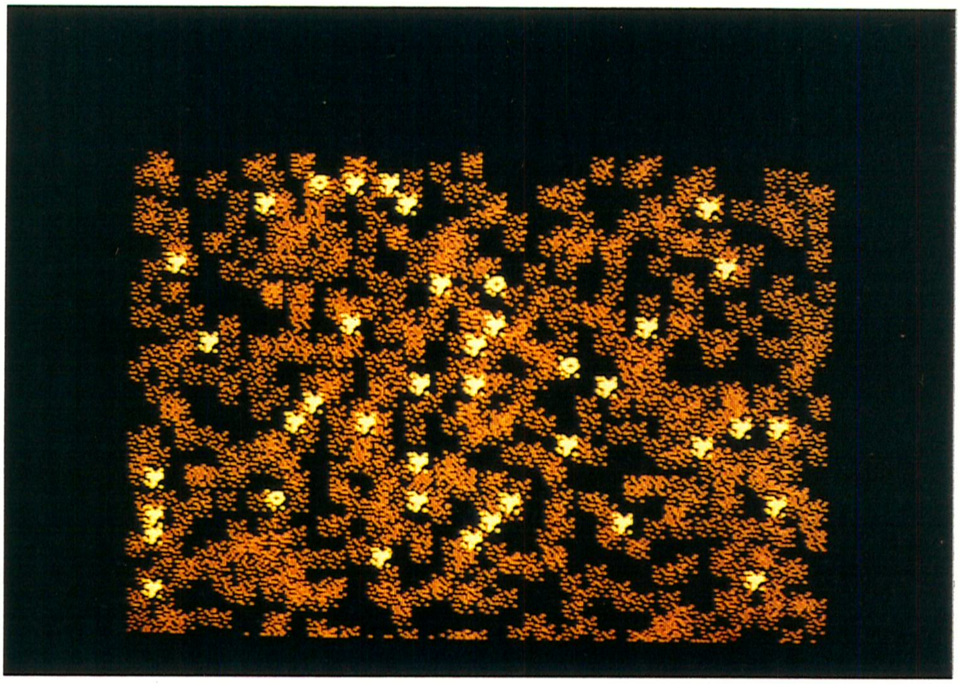


Plate 5.2. Typical background in Experiment 1b with conspicuous prey. Frequency of Prey 1 (circles) = 0.1, frequency of Prey 2 = 0.9.

trial was stopped after 10 prey had been detected, whilst at all other densities the trials were stopped when 20 prey had been found. Beta was calculated from the mean number of each prey type remaining after the eight trials. Although subjects were randomly assigned to the set of trials and within each frequency class the densities were presented in a random order, the trials with prey 1 frequency of 0.9 were carried out first. The 80 subjects used in this experiement were staff and students from the Department of Biology at the University of Southampton, as in the previous experiment.

RESULTS

The effect of prey frequency

The results for experiments 1a and 1b are shown in Tables 5.1 and 5.2 and Fig. 5.4. For the matching background (Fig. 5.4a), the positive slope of the regression line of B on frequency is statistically significantly different from zero ($t = 3.80$, d.f. = 68, $P < 0.001$), and the regression is not significantly improved by the inclusion of a quadratic term ($F = 0.0468$, d.f. = 1,68, N.S.). No such difference from zero slope was detected when the background made the prey conspicuous (Fig. 5.4b) ($t = 0.282$, d.f. = 48, $P > 0.1$). Additionally, the slopes of the two regression lines are significantly different (d of the normal distribution = 2.835, $P < 0.01$). It is therefore clear that selection occurred only when the prey were cryptic, and that this selection was apostatic.

The effect of frequency-independent prey preference

The mean value of B [prey 1] when the prey were presented in equal numbers was 50.2 when the prey were cryptic and 44.6 when conspicuous. This difference in selection was statistically significant ($t = 2.241$, d.f. = 15, $P < 0.05$). These deviations from 45, the value expected assuming no selection, were significant when the prey were cryptic ($t = 0.253$, d.f. = 9, $P < 0.005$) but not when conspicuous ($t = 0.253$, d.f. = 6, $P > 0.5$). There is thus evidence that prey 1 were preferred when both prey were cryptic but not when they were conspicuous.

Table 5.1. Results form Experiment 1a; arcsine transformed Beta selection coefficients obtained for prey 1 at different initial frequencies of prey 1, where both prey are cryptic.

FREQUENCY OF PREY 1

	0.5	0.10	0.25	0.50	0.75	0.90	0.95
	52.6	54.4	56.1	48.7	50.7	72.6	49.6
	00.0	46.4	49.7	57.4	59.5	56.7	64.7
	39.2	54.4	48.6	36.6	47.2	90.0	52.1
	55.2	61.5	49.0	51.6	54.9	46.2	75.3
	35.9	15.9	47.0	54.9	45.6	56.7	45.0
	47.5	50.6	46.4	48.7	58.2	51.1	90.0
	42.2	50.5	42.2	57.8	53.1	56.7	36.8
	52.6	49.1	44.3	52.8	54.3	43.9	47.2
	45.0	42.0	43.6	48.7	48.9	52.4	45.0
	55.2	49.1	44.3	45.0	58.2	65.4	61.0
Mean	42.5	47.4	47.1	50.2	53.1	59.2	56.7
S.E.	5.18	3.86	1.27	2.00	1.53	4.35	5.13

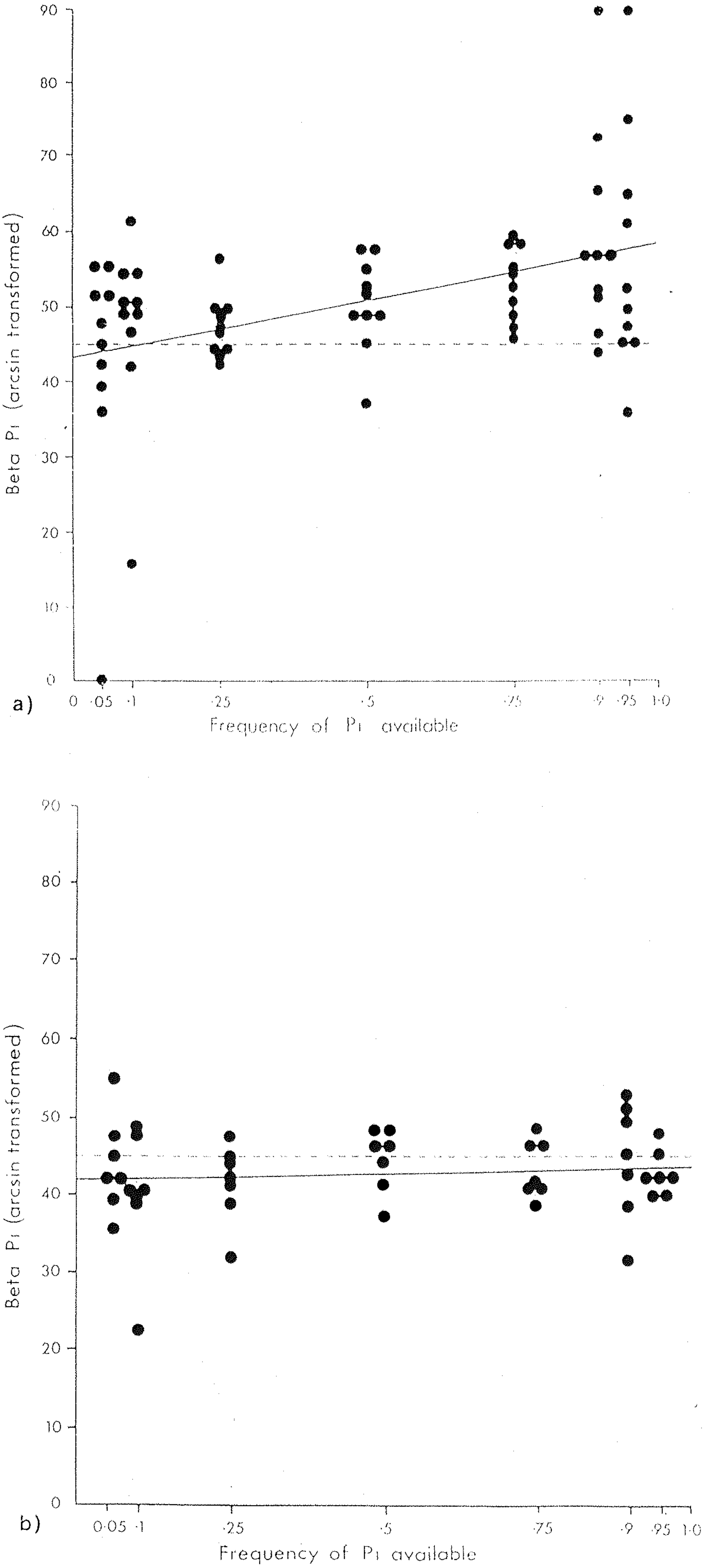
Beta values for each subject are based upon the mean numbers of prey remaining over eight trials.

Table 5.2. Results from Experiment 1b; arcsine transformed Beta selection coefficients obtained for Prey 1 at different initial frequencies of Prey 1 where both prey are conspicuous.

	FREQUENCY OF PREY 1						
	0.05	0.10	0.25	0.50	0.75	0.90	0.95
	39.2	40.5	45.0	37.3	38.3	31.4	42.3
	55.2	39.5	32.3	48.1	41.6	49.2	47.8
	42.2	40.5	47.7	46.5	46.4	45.0	45.0
	47.7	38.9	41.5	46.0	40.9	51.1	42.3
	35.9	47.8	38.6	48.6	48.5	52.7	39.7
	45.0	49.2	42.2	41.4	46.4	42.2	42.2
	42.2	22.5	44.3	44.4	40.9	38.1	39.8
Mean	43.9	39.8	41.6	44.6	43.3	44.2	42.7
S.E.	2.37	3.29	1.90	1.52	1.43	2.89	1.08

Beta values for each subject are based upon the mean numbers of prey remaining over eight trials.

Fig. 5.4. Selection against prey 1 in relation to frequency: (a) experiment 1a - both prey cryptic: $y = 43.50 + 14.77x$, $t = 3.80$, d.f. = 68, $P < 0.001$. b) experiment 1b - both prey conspicuous; $y = 41.94 + 1.92x$, $t = 0.828$, d.f. = 48, $P > 0.1$.



The effect of crypsis and experience on prey capture rate

Mean trial completion times (i.e. the time taken to 'predate' 20 prey items) for trials 2 and 9, at each frequency and in both cryptic and conspicuous experiments are presented in Table 5.3 and Fig. 5.5. The results show that firstly, in both the 2nd and last (9th) trials the subjects took significantly longer to complete trials with cryptic prey than equivalent trials with conspicuous prey, irrespective of frequency (see Table 5.4). This suggests that the subjects' capture rates were slowed down by perceptual limitations when increased visual scrutiny was required to detect the prey. However, because comparision of the experiments indicates that capture rate decreased by only 3.67 - 29.5 % when the prey were conspicuous, the majority of the prey capture time must have been due to prey handling (i.e. deletion with the light pen).

Secondly, in both cryptic and conspicuous prey experiments, trial completion times were significantly lower in the 9th trials than the 2nd irrespective of frequency (see Table 5.5). This effect of experience suggests that the subjects were learning and thereby increasing their capture rates. However as this effect was also apparent in the conspicuous trials this suggests that learning involved some process other than (or as well as) improved perception of the prey. In order to investigate this further the rate of improvement between the 2nd and 9th trials was measured by calculation of a beginning/end ratio (as used by Dawkins (1971a); Lawrence (1985a)). For each frequency and subject the 2nd trial completion time was divided by the 9th trial completion time. Thus a value greater than 1 indicates a greater capture rate in the last (9th) trial. Fig. 5.6 summarizes these results and Table 5.6 presents the associated analysis of variance. Although all values indicate that capture rates were faster in the last trial there was no significant difference in capture rate improvement between trials with cryptic or conspicuous prey.

The relationship between apostatic selection and prey capture rate

In order to test whether apostatic selection increased the rate of prey capture (or *vice versa*), the trial completion times

Table 5.3. Mean trial completion times (seconds) for cryptic and conspicuous prey experiments (1a and 1b) obtained at different initial frequencies of Prey 1. Standard errors are indicated in brackets.

Prey 1 Freq.	Trial 2		Trial 9	
	Cryptic	Conspicuous	Cryptic	Conspicuous
0.05	34.3 (4.65)	20.2 (1.82)	25.1 (2.62)	17.7 (0.74)
0.1	35.2 (3.87)	22.8 (2.60)	24.8 (2.03)	18.6 (1.89)
0.25	41.2 (6.37)	21.5 (2.08)	26.1 (4.92)	19.8 (3.07)
0.5	34.0 (4.05)	29.4 (3.76)	31.2 (2.80)	25.0 (2.94)
0.75	34.0 (3.74)	25.8 (3.00)	25.3 (2.78)	23.5 (2.89)
0.9	32.2 (3.03)	27.6 (2.47)	29.2 (2.52)	21.5 (2.56)
0.95	27.5 (1.34)	26.6 (3.09)	24.5 (1.64)	23.6 (3.08)

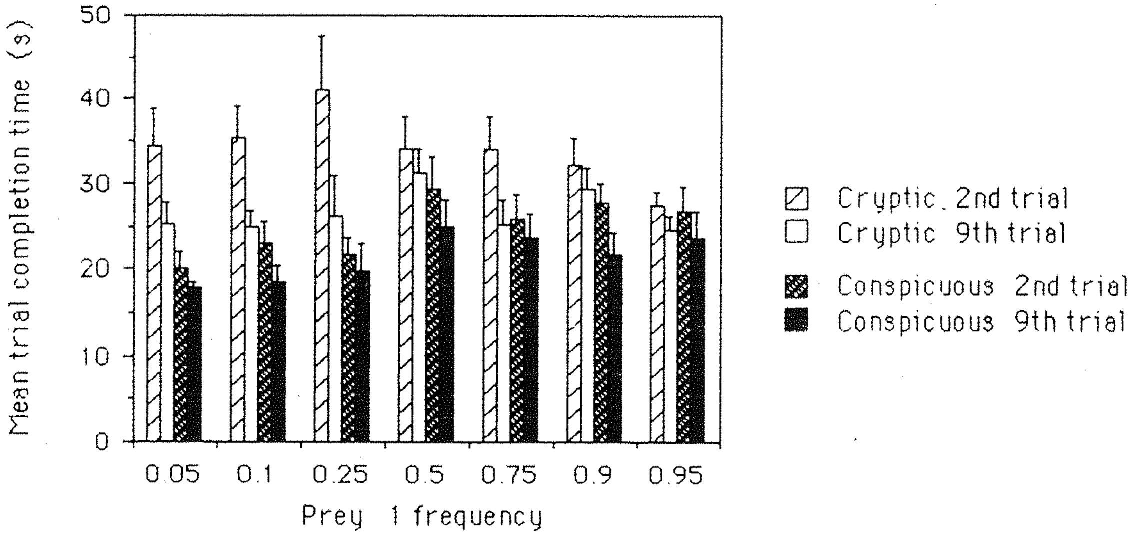


Fig. 5.5. Mean completion times of 2nd and 9th trials in experiments with cryptic prey (1a) and conspicuous prey (1b),) for each initial prey frequency. Standard errors are indicated as vertical bars.

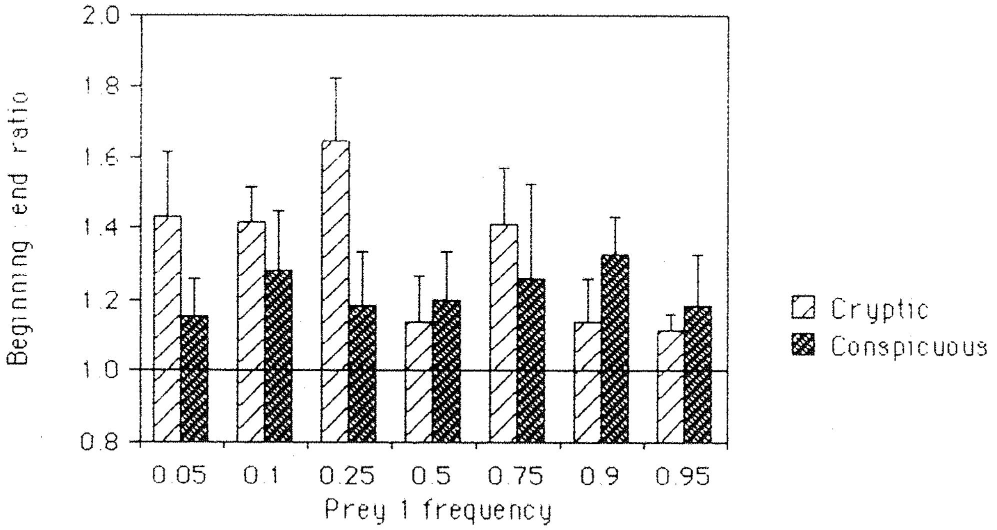


Fig. 5.6. Mean beginning/end ratios for cryptic (1a) and conspicuous (1b) prey experiments, for each initial prey frequency. Standard errors are indicated as vertical bars. Values above 1 indicate an increase in mean capture rate between the 2nd and last trial.

Table 5.4. Two-way analysis of variance of the effects of crypsis and prey frequency on trial completion time.

2nd Trial times

SOURCE	d.f.	SS	MS	F	P
Subgroups	13	349.66	268.82		
Crypsis	1	2276.16	2276.16	19.536	**<0.01**
Frequency	6	326.87	54.48	0.467	>0.05
Interaction	6	891.62	148.60	1.270	>0.05
Error	105	12233.71	116.51		
Total	118	15728.38			

9th Trial times

SOURCE	d.f.	SS	MS	F	P
Subgroups	13	1506.24	115.86		
Crypsis	1	790.44	790.44	11.749	**<0.01**
Frequency	6	532.52	88.75	1.319	>0.05
Interaction	6	183.27	30.545	0.454	>0.05
Error	105	7064.11	67.28		
Total	118	8570.35			

Table 5.5. Two-way analysis of variance of the effects of experience and prey frequency on trial completion time.

Cryptic trials.

SOURCE	d.f.	SS	MS	F	P
Subgroups	13	1098.121	84.471		
Experience	1	296.565	296.565	5.92	**<0.05**
Frequency	6	753.236	125.539	2.51	>0.05
Interaction	6	48.318	8.053	0.16	>0.05
Error	84	4206.480	50.077		
Total	97	5304.600			

Conspicuous trials.

SOURCE	d.f.	SS	MS	F	P
Subgroups	13	2927.95	225.23		
Experience	1	1781.22	1781.22	14.810	**<0.01**
Frequency	6	595.50	99.25	0.825	>0.05
Interaction	6	551.23	91.875	0.764	>0.05
Error	126	15151.46	120.25		
Total	139	18079.41			

Table 5.6. Two-way analysis of variance of the effects of crypsis and prey frequency on trial completion time beginning/end ratios.

SOURCE	d.f.	SS	MS	F	P
Subgroups	13	0.2978	0.02291		
Crypsis	1	0.0372	0.0372	1.507	>0.05
Frequency	6	0.1132	0.0189	0.762	>0.05
Interaction	6	0.1472	0.0245	0.991	>0.05
Error	105	2.1260	0.0248		
Total	118	2.4238			

Log10 transformed ratios were used in the analysis.

of each subject were plotted against their combined Beta selection value for prey 1, for those trials where selection was apostatic (i.e. those with prey 1 frequencies of 0.05, 0.1, 0.9, and 0.95). These results are presented in Figs. 5.7 and 5.8. In both trials where prey 1 is common (0.9 and 0.95) regression analysis indicates a negative slope and this suggests that fast capture rates were associated with increased apostatic selection (i.e. increased predation of prey 1); however, neither departure from zero slope is significant. Negative slopes are also evident in the trials where prey 1 is rare (0.05 & 0.1). Conversely this suggests that faster capture rates were associated with decreased apostatic selection (i.e. increased predation of prey 1); however, again neither departure from zero slope is statistically significant. These results show that apostatic selection had no effect on prey detection rate and although the subjects tended to detect prey faster when detecting predominantly prey type 1 this was not statistically significant.

The effect of prey depletion within trials on selection

Prey depletion within trials could have had an important effect on selection if the subjects responded directly to prey frequency. In such a case the frequency-dependent selection measured at 50% exploitation may be lower than selection earlier in the trial. To test this, Beta values were calculated for each subject for the first and second halves of each trial. These values were then compared by paired t-tests. Separate Beta values were calculated for each trial because the frequencies of the remaining prey in the second halves of each subjects trials were not consistent between trials. Beta values were calculated in this way for trials with prey 1 frequencies of 0.25 and 0.75. Extreme frequencies were not analyzed because Beta estimates based upon selection of only 10 prey would be susceptible to high bias and variance. Trials where the prey were presented in equal frequencies were not analyzed because apostatic selection was absent. The mean Beta [prey 1] selection coefficients calculated for the two halves of each subject´s set of trials are presented in Table 5.7, with the results of the statistical analysis. Of the 20 t-tests summarized in Table 5.7 only one is significant at the 0.05 probability level. Neither is there any evidence of a trend in the direction of differences between the Beta values derived

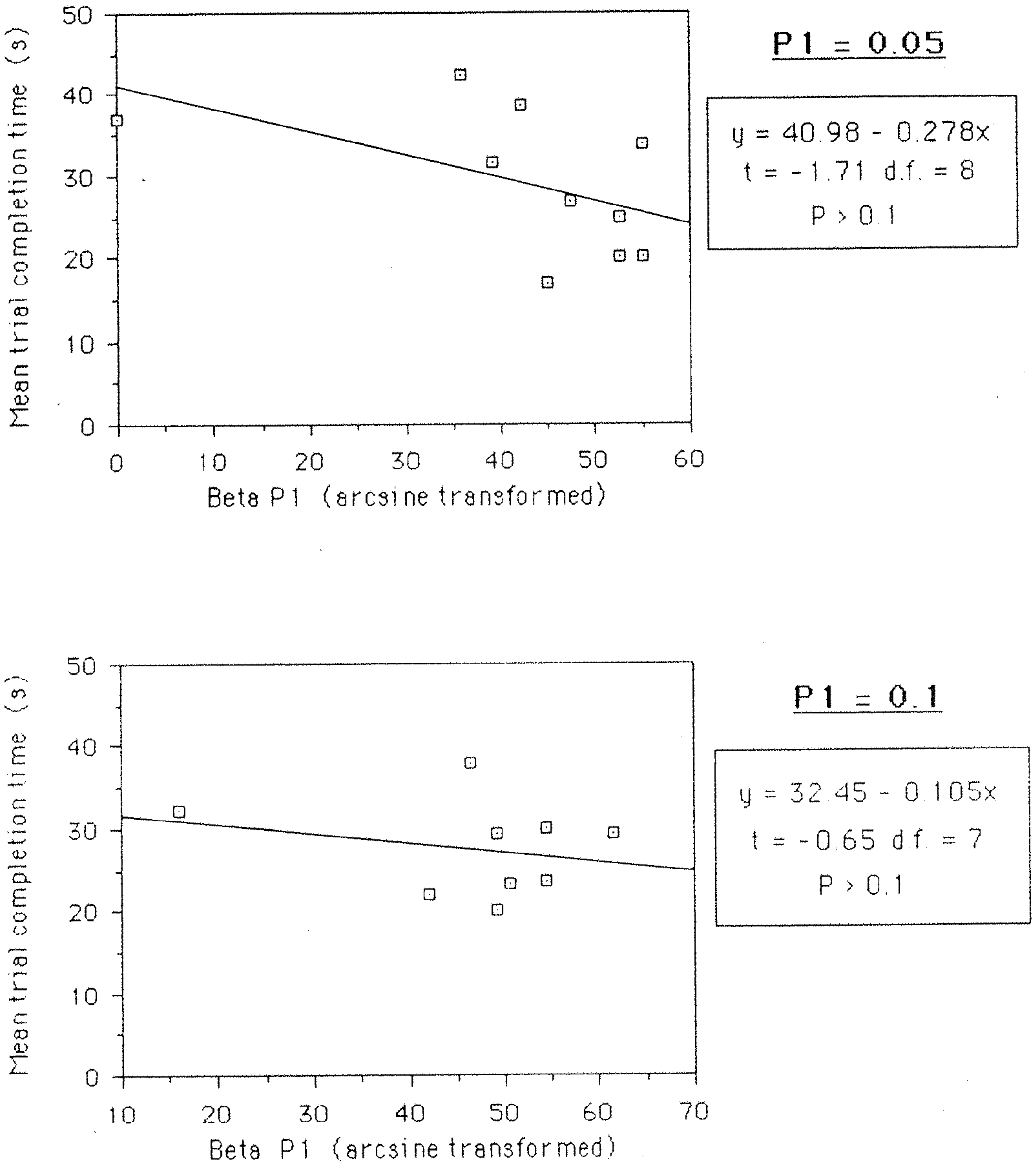


Fig. 5.7. Mean trial completion times in experiment 1a, in relation to selection against prey 1, in trials with initial prey 1 frequency of 0.05 and 0.1. An increase in apostatic selection is indicated by a decrease in Beta (prey 1).

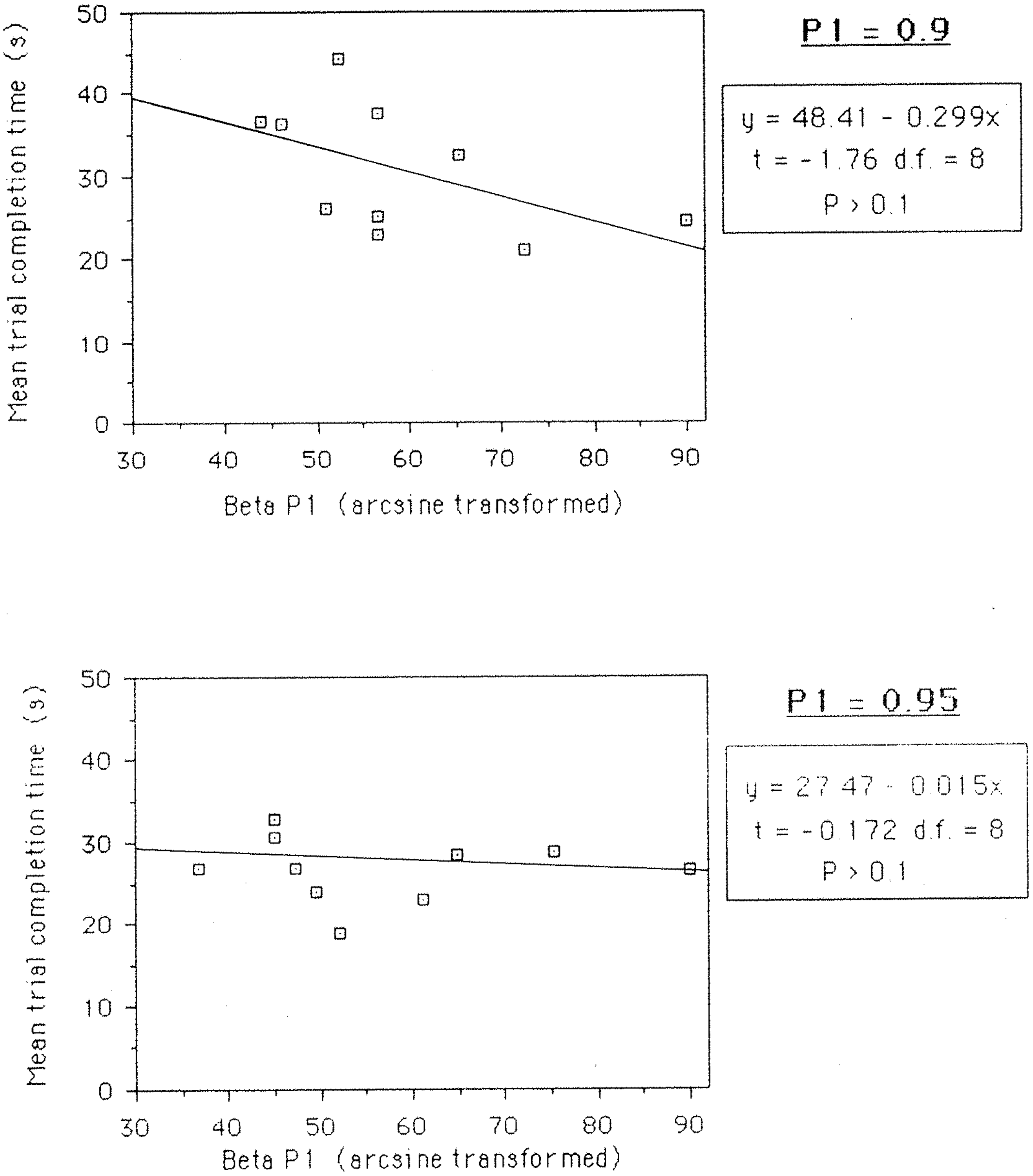


Fig. 5.8. Mean trial completion times in experiment 1a, in relation to selection against prey 1, in trials with initial prey 1 frequency of 0.9 and 0.95. An increase in apostatic selection is indicated by a increase in Bete (prey 1).

Table 5.7. Comparison of Beta (arcsine transformed) selection coefficients (for prey 1) calculated after selection of 10 and 20 prey.

a) Initial prey 1 frequency = 0.25

Subject	Mean Beta 10 prey	Mean Beta 20 prey	Mean Difference	t	P
1	57.07	54.21	-2.86	-0.611	>0.5
2	56.28	39.53	-16.7	-2.264	<0.1
3	50.64	46.14	-4.53	-2.495	<0.05
4	46.24	49.02	2.78	0.456	>0.6
5	48.68	44.18	-4.50	-1.021	>0.3
6	37.86	41.92	4.06	0.287	>0.7
7	38.47	42.82	4.35	0.814	>0.4
8	44.56	38.79	-5.77	-0.686	>0.5
9	66.48	67.27	0.79	0.159	>0.8
10	42.72	44.35	1.63	0.575	>0.5

b) Initial prey 1 frequency = 0.75

Subject	Mean Beta 10 prey	Mean Beta 20 prey	Mean Difference	t	P
1	62.72	47.19	-15.5	-2.058	<0.1
2	59.51	65.86	6.34	0.672	>0.5
3	47.89	50.68	2.78	0.400	>0.7
4	55.82	61.93	6.11	0.652	>0.5
5	44.89	48.07	3.18	0.710	>0.5
6	60.88	68.50	7.62	0.869	>0.4
7	52.45	58.13	5.69	0.675	>0.5
8	62.72	55.85	-6.87	-0.616	>0.5
9	56.63	48.60	-8.04	-1.018	>0.3
10	68.18	61.24	-6.93	-0.733	>0.4

t = Student's 't' value calculated by pairwise comparison.
P = significance of 't' for 7 degrees of freedom.

from the first and second halves of the trials. Therefore, there is no evidence that selection changed between the first and second halves of each trial for those trials analyzed.

The effect of experience on prey selection between trials

For each frequency a mean Beta [prey 1] value for each trial (except trial one) was calculated from the mean number of each prey type selected, with the subjects classed as replicates. This was then plotted against trial order and the effect of experience (as reflected by trial order) investigated by regression analysis. Fig. 5.9 presents the plots of Beta selection coefficents against trial order and Table 5.8 summarises the statistical analyses. The analyses show that the degree of apostatic selection decreased with successive trials in the three sets of trials when prey type 1 was less common than prey type 2 (Beta increased with trial order), and in two of the sets of three trials when prey type 2 was common (Beta decreased with trial order). However, although this is some evidence that experience was directly related to a decrease in apostatic selection, only one regression was statistically significant and therefore the results do not indicate a clear relationship between the degree of apostatic selection and experience. There is also no evidence that the frequency-independent preference for prey 1 changed with experience, because there was neither a consistent change in direction of selection across all frequencies with increased experience, nor a significant change when the prey were at equal frequencies.

The effect of prey density on selection

The results from experiment 2 are summarized in Table 5.9 and Fig. 5.10. Regression analysis of the effect of prey density on the degree of selection indicates that in those trials where prey 1 was more common than prey 2 (P1 frequency = 0.9), the degree of apostatic selection decreased as the density increased. This effect was statistically significant. Furthermore, below prey densities of 80 prey per screen, selection was clearly against Prey 1; however, this effect was reversed at the highest density of 100 prey per screen. Selection was consistently against Prey 1 in trials where the prey were presented in equal frequencies and

Fig. 5.9. The effect of trial order on selection against prey 1 in experiment 1a (with cryptic prey) for each initial prey frequency. Trial 1 data is omitted from the analysis. P1 = initial frequency of prey type 1. See Table 5.9 for regression analysis results.

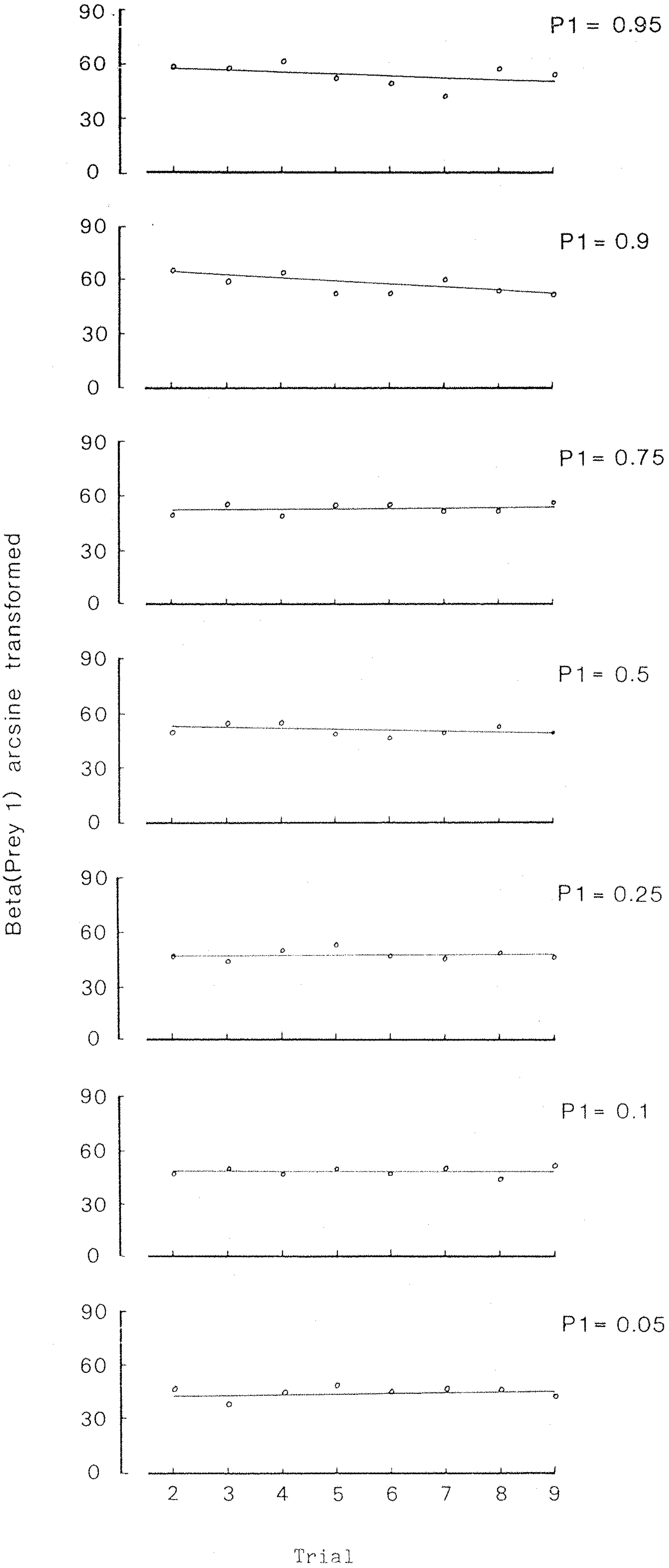


Table 5.8. Regression analysis of the effect of trial order on the selection of cryptic prey at different initial prey frequencies. Initial prey population = 40.

P1 Freq.	Regression Equation	r^2	t	P
0.05	$y = 44.00 + 0.210\ x$	0.0216	0.3640	>0.1
0.1	$y = 48.31 + 0.016\ x$	0.0003	0.0401	>0.1
0.25	$y = 47.77 + 0.069\ x$	0.0040	0.1557	>0.1
0.5	$y = 52.65 - 0.349\ x$	0.0882	-0.7602	>0.1
0.75	$y = 51.13 + 0.382\ x$	0.0990	0.8121	>0.1
0.90	$y = 65.52 - 1.567\ x$	0.4639	-2.2788	<0.1
0.95	$y = 59.24 - 0.921\ x$	0.1502	-1.0301	>0.1

P1 Freq. = initial frequency of prey 1 available.
r^2 = coefficient of determination.
t = t value for departure of regression from zero slope.
P = significance of departure from zero slope for 7 degrees of freedom.

Table 5.9. Results from Experiment 2; arcsine transformed Beta selection coefficients obtained for Prey 1, at different densities and at Prey 1 frequencies of 0.9 and 0.5.

	Density (prey/screen)				
P1 Frequency	20	40	60	80	100
0.9	51.09	45.0	45.0	77.55	38.3
	58.23	60.28	55.2	40.76	45.0
	62.48	39.48	46.25	41.76	45.0
	47.9	51.09	50.37	45.0	45.0
	39.48	70.53	47.56	68.77	52.9
	90.0	46.4	53.5	45.0	29.09
	54.49	46.4	55.2	51.56	38.25
	58.2	49.5	53.5	41.76	43.91
Mean	**57.67**	**51.08**	**50.82**	**51.52**	**42.18**
S.E.	6.07	3.48	1.45	4.94	2.48
0.5	61.44	56.33	47.21	32.48	49.42
	47.07	49.65	51.44	53.76	47.81
	52.22	52.22	53.40	47.91	45.8
	54.28	48.10	53.40	47.91	45.8
	47.07	54.79	52.52	47.08	48.08
	52.22	48.08	56.97	43.76	52.66
	65.51	51.19	46.77	50.82	51.44
	56.33	45.52	52.07	51.66	59.74
Mean	54.52	50.74	51.72	46.92	50.09
S.E.	2.29	1.29	1.19	2.33	1.62

Beta values for each subject are based upon the mean numbers of prey remaining over eight trials.
S.E. = standard error.

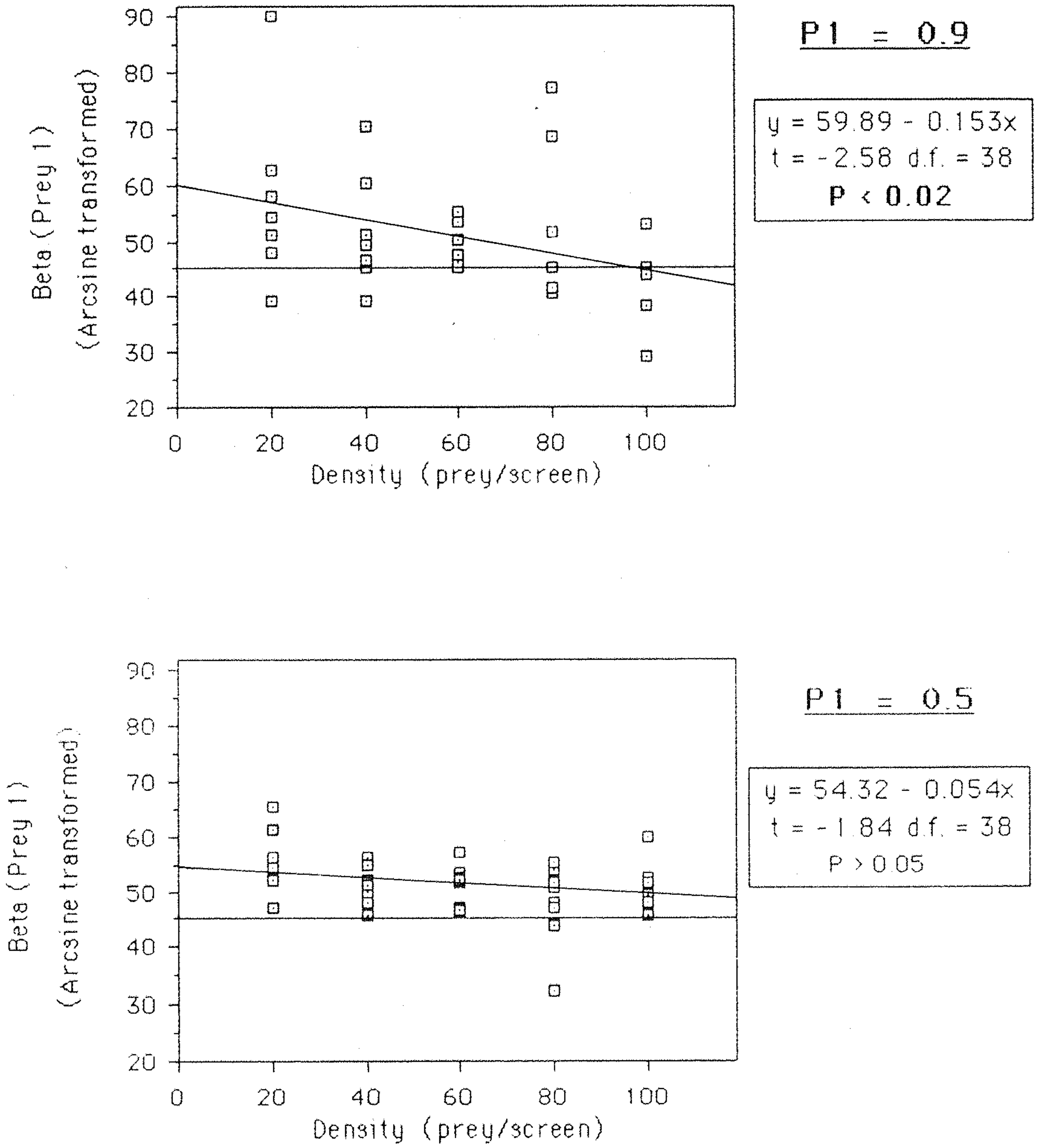


Fig. 5.10. The effect of prey density on selection against prey 1 in experiment 2 for trials with initial prey 1 frequencies of 0.9 and 0.5. The horizontal line is the relationship expected in the absence of selection.

there was no significant density effect on the degree of selection against Prey 1. However, a comparison of the two regression lines indicates that there was no difference in slope between the trials at different frequencies (z = 1.496, P > 0.1).

In order to test the effect of frequency on the overall selection (i.e. to test for apostatic selection) an analysis of covariance was carried out, with density as the covariate. After adjustment for the covariate there was no significant difference in least-square means between the trials carried out at the two frequencies (where P1 = 0.9, least-square mean = 50.67, S.E. = 1.34; where P1 = 0.5, least-square mean = 51.1, S.E. = 1.34; significance of difference between means, P = 0.832).

These results indicate that at both of the prey frequencies tested, selection decreased linearly as density increased. Furthermore, selection against Prey 1 was not apostatic when Prey 1 was common. Therefore, this suggests that increases in prey density affected the frequency-independent component of selection. Because of the absence of apostatic selection, the effect of density on the frequency-dependent component of selection cannot be established.

DISCUSSION

Frequency-dependent selection

In experiments 1a and 1b frequency-dependent selection was clearly demonstrated by humans selecting cryptic ´prey´. The magnitude of this effect was such that both prey were at a selective advantage when rare. However, frequency-dependent selection was not detected when the prey were conspicuous.

Relevance of the results to predators in general

The relevance of these results to behavioural models in general may be questionable, because of the disparities in perception and cognition between humans and other predators. However, the perceptual abilities of humans are thought to be similar to those of birds (Suthers 1977; Blough 1979), although their colour perception maybe more accute (Pumphrey 1948) and accommodation (speed of focusing) faster than ours (Schaeffel & Howard 1987). However, the greatly different cognitive abilities of humans and other predatory mammals and birds pose more serious pitfalls regarding interpretation of these results. The complicating factors of human information processing and interpretation might be expected to override any apostatic behaviour. Additionally the lack of reward for detecting prey might result in 'unnatural' behaviour. For example, the subjects might not attempt to maximize their capture rates and thereby feed sub-optimally. They might also respond to novelty and sample alternative prey (or objects) more than a real predator would. These factors would be expected to reduce any frequency-dependent effect. Clearly the apostatic selection detected when the prey were cryptic indicates that even if such complicating factors were present, they did not obscure frequency-dependent selection. Therefore the evidence for apostatic selection was probably in spite of, rather than because of, the differences in cognitive abilities between humans and animals.

Evaluation of possible behavioural mechanisms causing frequency-dependent selection

Greenwood (1984) has listed many potential proximate causes of frequency-dependent selection. Of these, and assuming that the subjects behaved in a way that maximized their 'feeding' efficiency, only those mechanisms involving: (1) some effect of prey handling or (2) the visual detection of the prey could account for the frequency-dependent selection when the prey were cryptic. All the other mechanisms depend on properties that the 'prey' did not have, such as differences between the morphs in their spatial distribution and profitability.

Handling properties (i.e. the techniques required to subdue and consume prey, or in this case delete prey with the light pen) may cause frequency-dependent selection if predators have to learn to handle different types of prey, and if these prey differ in their required handling techniques. Commoner prey will be encountered more frequently and therefore predators will learn to handle them more efficently than rare forms. Handling experience will thus result in a relatively greater reduction in the handling costs of common prey and this will therefore lead to an increase in their profitability. In such a situation it might benefit a predator to select common prey alone. Indeed the benefit of being a specialist feeder compared to a generalist has been demonstrated in jackdaws (*Corvus monoedulis*) (Partridge and Green 1987). Furthermore, greater success in handling common prey through experience has been shown to produce frequency-dependent predation in real predators (Lawton, Beddington and Bonser 1974; Bergelson 1985). The same might apply to humans deleting prey images, if different techniques were required to use the light-pen on the two prey types. However, if this was a causal mechanism, frequency-dependent selection would be expected even when the prey were conspicuous. The results of experiment 2 clearly show that this was not the case.

The absence of frequency-dependent selection when the prey were conspicuous (experiment 2) indicates that the behavioural basis of the observed selection when the prey were cryptic must have involved some visual property of the prey. Assuming that the subjects were behaving in a manner that maximized their detection effeciency, three possible mechanisms could account for these results:

(1) Common prey were selected preferentially because it reduced the searching costs of image processing (Greenwood 1984).

(2) The subjects adopted an optimal search rate which resulted in a reduction in the probability of detecting rare prey (Gendron and Staddon 1983; Greenwood 1984).

(3) Specific search images were developed for the common prey only, or only partially for the rare prey (Clarke 1962a).

In these experiments the maximization of feeding efficiency could have been achieved simply by maximizing feeding rate, because the prey were randomly distributed and had no real value (or, at least had an equal arbitary value). Evidence from Fig. 5.5 and Table 5.3 suggests that subjects did maximize their feeding rates. Capture rates (as estimated by trial completion time) were significantly faster when the prey were conspicuous (Table 5.4) and capture rates were faster in later trials (Table 5.5). These observations suggest that the subjects were ´trying´ to maximize their feeding rates and that crypsis and experience were limiting and improving factors respectively.

Although all three mechanisms predict frequency-dependent selection to be absent when prey are conspicuous they make different predictions regarding the form of the frequency-dependent response, changes in prey capture rate and effect of experience. Comparisons of the results may therefore reveal which (if any) of these behaviours were occurring in the experiments.

The simplest explanation is that the subjects preferred common prey (Clarke 1962a). The functional basis of this might be that the costs of visual processing are reduced (Greenwood 1984). Clarke predicted that this behaviour would result in greater frequency-dependent selection on those prey that were conspicuous, because the visual differences between morphs would be accentuated in such circumstances. However, there is no direct evidence of such an effect and although many studies have detected frequency-dependent selection on conspicuous prey (e.g. Allen & Clarke 1968; Allen 1972, 1974, 1976; Manly, Miller & Cook 1972; Fullick & Greenwood 1979), Bond (1983) and Cooper (1984) have demonstrated that the magnitude of selection is least when the prey are conspicuous. These studies and the results from my own experiments suggest that the difficulty of distinguishing prey items from the background is an important factor affecting frequency-dependent selection by predators. Despite this, a simple preference for common prey could explain the results if the red background in experiment 2 reduced the apparent visual difference between the two prey types. This is a likely possibility because the subjects could easily detect the prey in experiment 2 by simply responding to all yellow objects. Although this is a plausible explanation for the results when prey were conspicuous, it does not provide evidence that this mechanism contributed to the frequency-dependent selection observed when the prey were cryptic.

The model of Gendron & Staddon (1983) for predators searching for cryptic prey demonstrates that the optimal rate of search is based upon a trade-off between prey detection and frequency of encounter. When a predator is searching for two prey types that differ in their degree of conspicuousness the optimal rate of search increases with the frequency of the more conspicuous type and this may considerably reduce the chances of detecting the less conspicuous type. The model predicts that the most conspicuous type should always be selected to excess and this preference should be greatest when it is common. Thus frequency-dependent selection only occurs for the more conspicuous prey (Greenwood 1984). This model does not appear to apply to my results. Although there is evidence that prey type 1 (open circle) was more conspicuous (B [prey 1] = 50.2 when the two prey were presented at equal frequencies) it was not consistently preferred at all frequencies.

Differential search image formation has often been suggested as the underlying behavioural basis of frequency-dependent selection by predators (e.g. Clarke 1962a, Bantock, Bayley & Harvey 1974; Harvey, Birley & Blackstock 1975; Cornell 1976) despite the absence of direct evidence linking the two phenomena. Indeed, Guilford & Dawkins (1987) have thrown the existence of search image into doubt. These authors re-examined the studies of Dawkins (1971a), Pietriwicz & Kamil (1979), Lawrence (1985a,b) and Gendron (1986), previously thought to have provided strong direct evidence for search image development by predators. They argue that the results of these studies can be interpreted equally well as evidence for the search rate hypothesis of Gendron & Staddon (1983). Guilford and Dawkins suggest that search image development can only be demonstrated unequivocably when it is shown that a predator improves it´s ability to detect cryptic prey, with an associated increase in search rate and a decrease in the ability to detect rare prey. Therefore evidence that search image development is a causal mechanism for frequency-dependent selection by predators can only be obtained from studies that incorporate these observations with the demonstration of frequency-dependence. To date this has not been achieved.

Neither search rate or the ability to detect prey were directly measured in this study and therefore there is no direct evidence that the acquisition of search images contributed to the observed frequency-dependent selection of cryptic prey. Despite this, the evidence discounting the optimal search rate hypothesis and the lack of evidence supporting the common prey preference hypothesis suggests that search image development is the most plausible explanation for the observed frequency-dependent selection. However, it is possible that the frequency-dependent selection was a result of a combination of behavioural mechanisms. Indeed inspection of the selection/frequency response curve (Fig. 5.4) suggests that at intermediate frequencies apostatic selection occurred at low magnitude and only became excessive (in some subjects) at high prey frequencies. One plausible interpretation of this might be that search image development occurred throughout and caused a slight frequency-dependent response, whilst only at high prey frequencies did some subjects adopt a selective preference for common prey. At such frequencies the benefits of reducing processing costs would be maximized.

The functional basis behind all the mechanisms discussed is the necessity to increase prey capture rate. However, the absence of a positive correlation between the degree of apostatic selection and capture rate (Figs. 5.7 and 5.8) suggests that such an effect was either absent or unimportant. However, Weale, Tucker & Allen (1988) did detect higher capture rates when humans concentrated on selecting the common forms of a tetramorphic prey population. The experimental design may also be inappropriate for detecting such effects because handling time was the major factor limiting prey capture rate. Therefore handling ´noise´ may have obscured more subtle differences between the subjects foraging strategies.

Changes in selection within trials

The analytical technique of Manly (1973) for trials where prey are not replaced has been criticized on the grounds that it assumes selection to be constant throughout the trial (Greenwood & Elton, 1979). This may not be a valid assumption if the predator´s behaviour is modified by prey experience, or directly related to prey frequency. Comparison of the Beta values of the 1st and 2nd ten prey selected in each trial of experiment 1 show that there was no change in selection between these periods of the trials. Therefore Manly´s model appears to be valid for this aspect of the experiment and under these conditions. However, exploitation of prey beyond 50% of the original population may lead to changes in predator behaviour, particularly if the original population is small.

Changes in selection between trials

None of the previous studies on frequency-dependent selection have investigated the effects of experience, despite its potential importance. Such information would be valuable for examining the behavioural basis of selection. More importantly if frequency-dependent selection decays with experience then it is unlikely to be important in the maintenance of polymorphisms in nature. If this is the case then the results of previous experiments may only represent a transient stage of predatory behaviour that has little evolutionary importance. This study shows that within the limited time span investigated there is no evidence that selection changed with increased experience.

The effect of density on selection

It has been suggested that apostatic selection should be strongest when prey occur at intermediate densities and absent at low and high densities (Tinbergen 1960; Clarke 1962a). This idea is based on the assumption that apostatic selection is due to search image formation. Tinbergen (1960) postulated that in such circumstances and where prey are at low densities, predators will not encounter them sufficiently often to form search images. Conversely, where prey are at high densities then the encounter rate will be so great that either search images will not be important, or they may be formed for all prey types. However, there are now known to be many potential causes for apostatic selection (Greenwood 1984), and the effect of density on mechanisms other than those involving search images are poorly understood.

To date, although there is good evidence that selection becomes anti-apostatic at very high prey densities (Pielowski 1959,1961; Allen 1972; Ohguchi 1978; Horsley *et al*. 1979; Allen & Anderson 1984; Greenwood, Johnston & Thomas 1984; Greenwood, Blow & Thomas 1984), there have been few experiments investigating the effect over moderate densities. Cook & Miller (1977) found that quail showed strongest apostatic selection at intermediate densities (2.5 prey m^{-2}). But further analysis of the data by

Greenwood, Elton & Miller (in prep) showed that (unlike this study), the frequency-independent component of selection was independent of density.

Willis *et al.* (1980) obtained similar results to this study, in experiments using domestic chicks feeding on coloured chick crumbs. They found that the frequency-independent component of selection varied with density. Furthermore, they failed to detect frequency-dependent selection, despite this being demonstrated in previous experiments using the same techniques (Fullick & Greenwood 1979; Greenwood, Wood & Batchelor 1981). Therefore, the effect of density on the frequency-dependent component of selection remained untested.

Experiments using wild birds feeding on pastry prey were carried out by Raymond (1987) and Horsley (1978) to investigate the effect of density on apostatic selection. However, both studies produced inconclusive results, due to birds carrying over learnt behaviours between trials in the former study and heterogeneity in behaviour between birds at different sites in the latter.

Clearly, at moderate levels density has no simple effect on apostatic selection and its investigation is not always straightforward. Although the data available consistently shows an inverse relationship between overall selection and density, the results are contradictory regarding which components of selection are affected. Therefore, until further experimental investigations are carried out, the underlying relationship between apostatic selection and prey density remains unclear.

CHAPTER 6

APOSTATIC SELECTION BY HUMANS: THE BEHAVIOURAL BASIS.

INTRODUCTION

The experiment described in the previous chapter provided good evidence that humans selected prey in an apostatic manner under the conditions tested. However, the experimental technique did not enable the identification of the causal mechanism, although it was almost certainly some effect of the searching behaviour. A major problem was that the light-pen required a certain amount of skill to operate and the resulting ´handling time´ accounted for the majority of time taken to complete each trial. Thus any subtle differences in prey capture rate caused by modifications in searching behaviour could have been obscured by proportionately greater variations in handling time. To overcome this problem a new experimental design was used. The prey and background elements were identical to those used in the previous experiments, but the subject was only required to decide whether a prey item was present or absent in a random sequence of ´frames´. Some ´frames´ had a prey item on the background, others did not. Thus the necessity to use the light-pen (and therefore handling behaviour) was eliminated. From this experiment the probability of detecting a prey was established together with the time taken to decide whether a prey item was present or absent.

Previous attempts to investigate search image development (Dawkins 1971a; Pietriwictz & Kamil 1979; Lawrence 1985a,b and Gendron 1986) were flawed because the results could not differentiate between the hypotheses of search image and search rate modifications as explanations of demonstrated improvements in the ability to detect cryptic prey (Guildford & Dawkins 1987). However, the experimental technique used here explicitly tests whether or not humans adopt search images or modify their search rate (or both) when searching for cryptic prey. It also tests whether there is a cost to searching for more than one prey type simultaneously.

Search image development can be detected by testing the following predictions of Guilford & Dawkins (1987). First, search image is considered to be specific to only one type of prey (Tinbergen 1960; Dawkins 1971; Lawrence & Allen 1983) and its development leads to a form of perceptual specilization. However, by concentrating on the specific configuration of the target prey, the predator reduces its ability to detect other forms of prey (Croze 1970; Kamil & Pietrewicz 1979). This 'interference' should not occur when predators improve their detection ability by modifying their search rate (Guilford & Dawkins 1987).

Second, although both search image development and search rate modification is expected to lead to an increased prey detection rate, this would be caused by perceptual specialization in the case of search image (Dawkins 1971a). In contrast, where search rate modification occurs a higher detection rate is caused by a decrease in the rate of search (Guilford & Dawkins 1987). Although the search rate of a predator cannot be measured directly (at least, without detailed measurements of eye movement), it can be indirectly assessed by measuring the amount of time taken to decide that a prey item is absent (i.e. the 'giving-up time'). This however, assumes that the 'giving-up time' is closely correlated with search rate. Although this assumption would be difficult to test, it does seem reasonable to assume that a subject who searches quickly will decide quickly whether or not a prey item is present.

Thirdly, Guilford & Dawkins (1987) state that the search rate hypothesis cannot give rise to apostatic selection whereas the development of a search image can, because interference reduces the risk of predation on rare prey. However, this is not entirely correct. According to the model of Gendron & Staddon (1983) (upon which the ideas of Guilford & Dawkins (1987) were based) 'potentially' apostatic selection may result from a change in search rate if the most conspicuous of a set of prey is also the most frequent (Greenwood 1984). This is because the optimal search rate is fastest when the more conspicuous prey is common and consequently the ability to detect the rare cryptic prey is lowest. Thus although the predator will always take an excess of conspicuous prey this will be more so when this prey is common rather that rare. Therefore, in experiments with sequences of two types of equally cryptic prey, apostatic selection provides evidence for search image development, provided other mechanisms for frequency-dependent selection do not apply.

METHODS

Experiment 1

The basic technique was similar to that described in the previous chapter, in which computer generated prey images were presented on a VDU screen, upon a background against which they were cryptic, to a series of naive human subjects ('predators'). However, unlike the previous experiments, only one prey item was presented in any one trial, and 'blank' trials were included in which prey were absent. Furthermore, the subjects were only required to decide whether a prey item was present on the screen and press the appropriate key to indicate its presence. (In trials with two prey types two different specific keys were used). Alternatively, as soon as a subject decided that no prey were present they pressed the key designated to indicate a blank screen. Blank trials were included to control for spurious correct responses (see under analysis below) and to provide estimates of the time taken by subjects to decide that prey were absent.

The computer program.

The programs were again written in BBC Basic to run on a BBC Model B (32 K) micro-computer linked to a C ub Microvitec colour monitor. The listings are given in Appendix 2. The prey types and background characters were as described in Chapter five and illustrated in Fig. 5.2. As before, the prey item (if present) and background characters were displayed within a window 21.5 cm wide by 15.5 cm high.

Whilst the background and prey were being generated by the computer all elements were the same colour as the screen and thus not detectable to the subject. After 11.25 s the distribution of prey and background was complete and the computer prompted the subject to press a defined key to start the trial. When commanded the computer redefined the prey and background characters to yellow making the display visible and thus enabling the subject to start searching the screen for a prey item. The VDU display was always set to maximum brightness to standardise the visual display. If the subject detected either prey type 1 or prey type 2 they pressed the keyboard keys labelled 1 and 2 as appropriate. Alternatively key 0 was pressed if the subject decided that no prey item was present. Once one of the three keys had been pressed the computer stopped the trial and recorded the subject's response. If the subject incorrectly pressed a key for a prey type that was absent then the computer emited a short 'bleep' to indicate the mistake. After 30 trials the program automatically ended the experiment and printed out the results for each trial (i.e. the prey type presented, the subject's response and the time elapsed between the start of the trial and each response).

Experimental procedure.

The first experiment consisted of three trials in which prey of the following type were present:

(a) Experiment 1a - prey type 1
(b) Experiment 1b - prey type 2
(c) Experiment 1c - both prey types 1 and 2

Each trial tested ten subjects, each of whom was presented with 30 frames. In experiments 1a and 1b 15 frames had a prey item present with the remainder (15) with no prey present (blank frames). In experiment 1c each prey type was presented singly in 10 frames. The remaining 10 frames were blank. Prey and blank frames were presented in a random order to each subject.

The subjects were 30 volunteers (5 males and 5 females in each set of trials) from the staff and students at the Medical and Biological Sciences Building, at the University of Southampton. Care was taken to ensure that each subject had no prior knowledge of the purpose of the experiment. Before each subject started his/her trials the program displayed a set of written instructions stating that "an arena will be displayed on the screen consisting of a yellow background with OR without a 'prey' item of the same colour". The subject was also instructed that the task was to search the screen for the prey item and immediately press the appropriate key (i.e. key 1 for prey 1) if they detected it. The instructions also indicated that they should press key 0 as soon as they decided that prey were absent. The instructions are presented in the program listings in Appendix 2. As in the previous experiments the subject was then shown an example of the prey simultaneously displayed against a blank (dark) screen for 10 s to counteract the possible effects of novelty (cf. Lawrence and Allen 1983).

After completion of their trial the subjects were asked whether they had knowledge of apostatic selection or switching behaviour. If they did then their results would have been disregarded in order to avoid potential bias. In fact, this was never necessary.

Experiment 2

The experiment was the same as described above for experiment 1c (where prey 1 or 2 were presented) with these exceptions. Firstly, prey were not presented in equal frequencies but in three sets of trials with prey 1 and 2 in ratios of either 5:1, 1:1 or 1:5. Secondly each subject was presented with 45 frames, of which 15 (33.3%) were blank (i.e. had no prey present). Thirdly, frames were presented on a Zenith (ZVM-1200 Series) monochrome monitor, with amber prey and background elements. Screen brightness and contrast was standardised between trials and the background and prey were presented in a screen window of 13 cm high x 20 cm wide. The sequence of prey in each set of frames was randomised by the computer program. As in the previous experiments 10 subjects were randomly ascribed to each set of trials, although these were staff from the British Trust for Ornithology, at Tring. The order in which the trials were carried out was also randomised.

Analysis.

In both experiments the detection probability (i.e. the total detected divided by the total presented) for each prey, over the entire trial was corrected to take account of subjects occasionally giving the correct answer when a prey item was present, although they had not detected it. Although these spurious correct responses are indistinguisable from valid correct responses, the overall detection probability can be corrected by use of the simple formula of Gendron & Staddon (1984):

$$PD_i = \frac{PD+ - PD-}{(1 - PD-)}$$

Where:

PD_i = Corrected probability of detecting prey type i

PD+ = Probability of detecting prey i presence when prey i was present

PD- = Probability of falsely detecting prey i when prey i was absent

(In trials with both prey, PD- was calculated from responses where both prey were absent).

Analysis of frequency-dependent selection was carried out using the method of Manly (1974) for experiments with replacement of prey. This method is appropriate because the prey were presented sequentially and therefore there was effectively no change in initial prey frequency. Corrected probabilities (as calculated above) were used in this analysis.

EXPERIMENT 1 RESULTS

The effect of successive prey encounters on detection ability.

Each subject's responses in Experiments 1a, 1b and 1c are summarized in Tables 6.1, 6.2 and 6.3 respectively. Figs. 6.1 and 6.2 show prey detection success for both prey types, in relation to the number of prey encounters for each set of trials. Although regression analysis indicates that in three of the four data sets, detection success was positively correlated to the number of encounters, in none of these cases was this effect statistically significant (Table 6.4). This suggests that there was no consistent improvement in the ability of the subjects to detect the prey over the course of their trials. Consequently there is neither evidence for the development of a search image nor the optimization of search rate. However, a rapid improvement in detection ability might have occurred as a result of the first successful encounter, in which case, regression analysis would be insensitive to this effect. To test for this, paired comparisons of the initial detection probability up to the first detection

Table 6.1. Summary of subject responses in Experiment 1a.

	Response						
Subject	1	+	0	?	PD	Dt	G-Ut
1	11	4	14	1	0.714	3.57	6.12
2	10	5	15	0	0.667	2.88	6.98
3	9	6	14	1	0.571	4.31	7.14
4	13	2	14	1	0.857	2.21	6.23
5	1	14	15	0	0.067	1.54	1.32
6	10	5	13	2	0.615	4.48	7.37
7	13	2	12	3	0.833	3.12	6.31
8	14	1	14	1	0.928	4.58	7.97
9	4	11	13	2	0.154	1.77	3.07
10	14	1	14	1	0.928	4.16	10.8

1 = Prey present and detected
+ = Prey present but not detected
0 = Prey absent and correct answer
? = Prey absent and incorrect answer
PD = Corrected probability of prey detection (see text)
Dt = Mean prey detection time
G-Ut = Mean give-up time in blank trials

Table 6.2. Summary of subject responses in Experiment 1b.

	Response						
Subject	2	+	0	?	PD	Dt	G-Ut
1	7	8	14	1	0.428	5.59	16.3
2	2	13	15	0	0.133	2.25	2.48
3	0	15	14	1	0	-	5.55
4	11	4	14	1	0.714	7.68	18.2
5	14	1	9	6	0.889	2.46	8.70
6	12	3	13	2	0.769	4.18	7.63
7	11	4	15	0	0.733	4.54	11.8
8	12	3	15	0	0.800	3.56	10.7
9	7	8	15	0	0.467	4.48	5.38
10	12	3	11	4	0.727	6.50	11.2

2 = Prey present and detected
+ = Prey present but not detected
0 = Prey absent and correct answer
? = Prey absent and incorrect answer
PD = Corrected probability of prey detection (see text)
Dt = Mean prey detection time
G-Ut = Mean give-up time in blank trials

Table 6.3. Summary of subject responses in Experiment 1c.

Subject	Response													
	1	2	0	+1	+2	-1	-2	?1	?2	PD1	PD2	DT1	DT2	G-Ut
1	9	5	9	1	5	0	1	0	0	0.9	0.444	9.00	6.51	13.9
2	6	6	9	4	4	0	1	0	0	0.6	0.555	1.87	2.17	3.06
3	10	5	7	0	5	2	1	0	0	1.0	0.444	6.64	7.52	12.1
4	8	9	9	2	1	1	0	0	0	0.778	0.9	7.60	10.4	21.8
5	7	4	7	3	6	1	2	0	2	0.667	0.25	3.81	7.97	5.80
6	8	1	9	2	9	0	1	0	0	0.8	0	2.50	2.81	4.23
7	9	0	6	1	10	2	2	1	0	0.875	0	6.56	-	8.52
8	0	0	10	10	10	0	0	0	0	0	0	-	-	1.49
9	0	0	10	10	10	0	0	0	0	0	0	-	-	0.69
10	8	0	10	2	10	0	0	0	0	0.8	0	3.71	-	4.10

1 = Prey 1 present and detected
2 = Prey 2 present and detected
0 = Prey absent and correct answer
+1 = Prey 1 present and undetected
+2 = Prey 2 present and undetected
-1 = Prey absent and key 1 pressed
-2 = Prey absent and key 2 pressed
?1 = Prey 2 present and key 1 pressed
?2 = Prey 1 present and key 2 pressed
PD1 = Corrected probability of prey 1 detection (see text)
PD2 = Corrected probability of prey 2 detection (see text)
Dt1 = Mean prey 1 detection time
Dt2 = Mean prey 2 detection time
G-Ut = Mean give-up time in blank trials

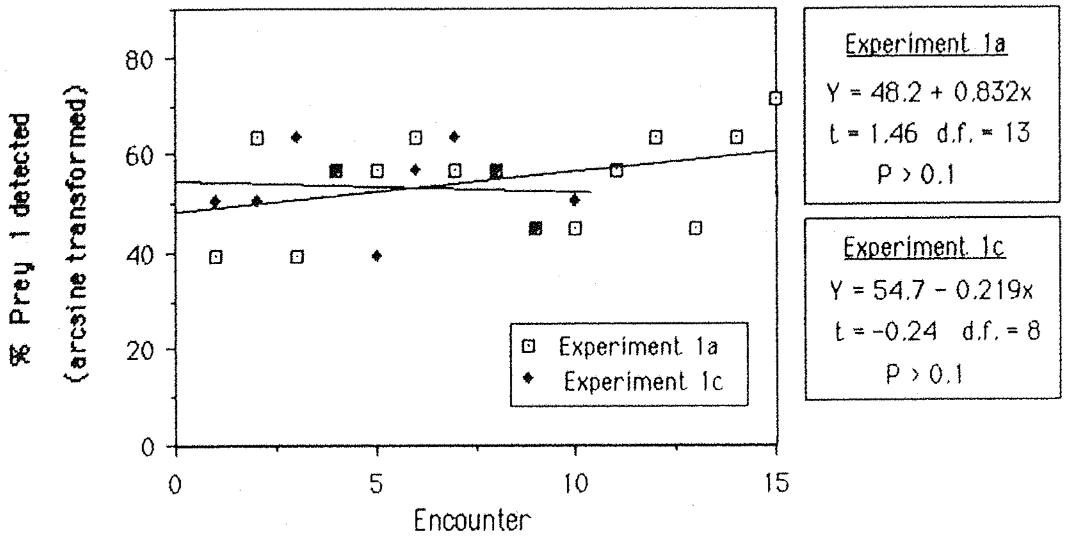


Fig. 6.1. The effect of encounters with Prey 1 on Prey 1 detection in single (1a) and double (1c) prey experiments.

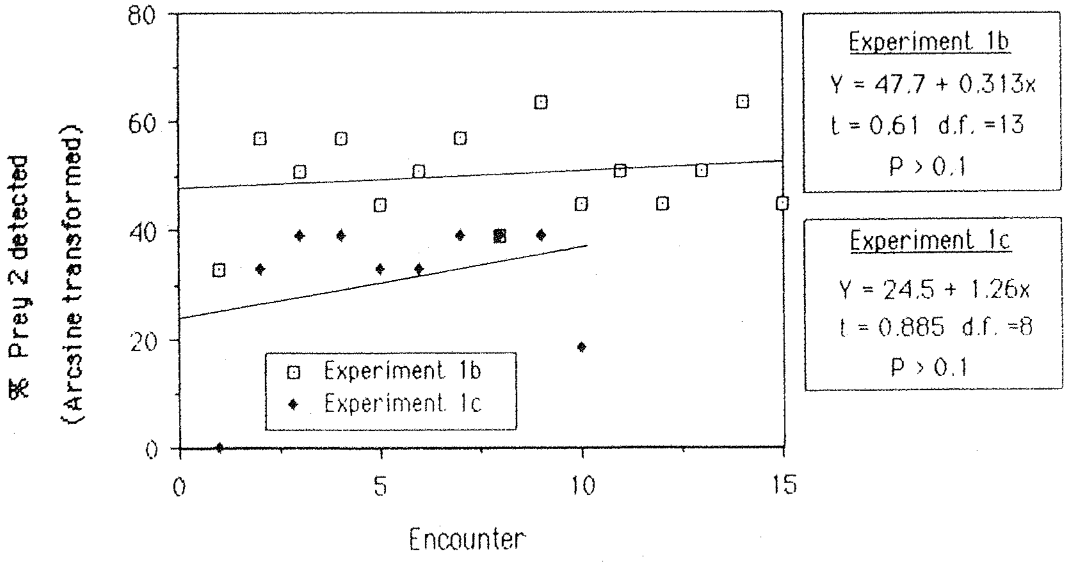


Fig. 6.2. The effect of encounters with Prey 2 on Prey 2 detection in single (1b) and double (1c) experiments.

Table 6.4. Regression analysis of the effects of successive prey encounters on prey detection success. Analyses are based upon arcsine transformed values.

Expt.	Prey type	Regression Equation	r^2	t	P
1a	1	$y = 48.19 + 0.832x$	0.141	1.464	>0.1
1b	2	$y = 47.68 + 0.313x$	0.027	0.606	>0.1
1c	1	$y = 54.68 - 0.219x$	0.007	-0.246	>0.1
1c	2	$y = 24.49 + 1.261x$	0.089	0.885	>0.1

with the detection probability over the remaining part of the trial were made (Table 6.5). This analysis showed no significant increase in the ability to detect prey after the first succesful encounter. However, in all but 2 cases the first detection occurred within the first three encounters and therefore the initial detection probability estimates are probably not accurate for these cases. Thus, the data cannot be reliably used to test for differences between detection rate before and after the first detection.

The effect of succesive prey encounters on detection rate

The acquisition of a search image or the optimization of search rate might lead to a change in detection rate (prey/s) rather than to a direct change in the proportion of prey detected. To test this, for each subject the initial prey detection rate (as measured over the first three encounters) was compared to the final detection rate (measured over the last three encounters). The results of the paired t-tests for each experiment are shown in Table 6.6. Although in each experiment the final detection rate was higher than the initial rate, only in Experiment 1c was this difference significant. However, the combined probability of the three experiments indicates that overall, subjects did increase their detection rate with succesive prey encounters.

The results presented so far suggest that the subjects did not learn to detect a higher proportion of prey over the course of the experiment although they did increase their overall prey detection rate. This may have been due in part to a 'trade-off' between an increased ability to detect prey and a faster search speed. As each subject learnt to detect the prey, they may have simply searched faster. Thus the proportion of prey detected would not be increased, although the overall searching efficiency is. Alternatively, the failure to increase the ability to detect prey could have been due to at least four other possible factors:

(1) The prey may have been either too difficult or too easy to detect, so that development of a search image or optimization of search rate had little or no effect.

(2) A search image or the acquisition of an optimal search

rate may have occurred virtually instantaneously when the prey were displayed *before* the beginning of the each subject's trial.

(3) The detection of prey may have been largely dependent on stochastic factors (for example, the chance positioning of the prey on the background) and thus, because of the small sample size, any changes in detection ability would have been masked by these random effects.

(4) Changes in the ability to detect these types of cryptic prey may not occur in the particular circumstances of these experiments.

Of these hypotheses, (1) is unlikely to apply because 60% of the subjects detected less than 80% of the prey and no subject detected all of them. Furthermore, the number of prey detected by each subject was positively correlated with the mean time spent searching (i.e. the mean give-up time) in all experiments (Fig. 6.3). In all cases, linear regression indicates that the slopes are positive and significantly different from zero. However, the inclusion of a quadratic term significantly improves the regression in Experiment 1b and 1c for prey type 1.

The effect of searching for two prey types

If there is a cost to searching for two prey types simultaneously, then it might benefit a predator to restrict searching to the most common prey, thereby creating apostatic selection (Greenwood 1984). Furthermore, this effect may be reinforced by search image interference against the rare prey. Additionally the capacity for search image formation may be limited to one or a few prey types. If a predator can form only one search image at a time, then again apostatic selection may occur as a result of search image interference (Guilford and Dawkins 1987).

The results show that in the double prey experiment, the proportion of errors was higher (Table 6.7). Although this suggests that there was a cost to searching for two types of prey, none of these differences is significant at the 5 % probability level. Also, significantly fewer prey type 2 were detected with

Table 6.5. Wilcoxon signed rank tests comparing initial detection probabilities (up to the first detection) with detection probabilities over the remaining parts of each trial, for prey types 1 and 2 in single prey experiments.

Prey type 1 (Expt. 1a).

Subject	1st Detection	Total Detections	Overall rate	Initial Probability	Remaining Probability
1	2	11	0.733	0.5	0.769
2	2	10	0.667	0.5	0.692
3	2	9	0.6	0.5	0.615
4	2	13	0.867	0.5	0.923
5	15	1	0.068	0.067	-
6	6	10	0.667	0.167	1
7	1	13	0.867	1	0.857
8	1	14	0.933	1	0.928
9	1	4	0.267	1	0.214
10	1	14	0.933	1	0.928

Non-zero differences = 9, Wilcoxon statistic = 15, P > 0.05

Prey type 2 (Expt. 1b).

Subject	1st Detection	Total Detections	Overall rate	Initial Probability	Remaining Probability
1	3	7	0.467	0.333	0.5
2	-	0	-	-	-
3	2	2	0.133	0.5	0.077
4	1	11	0.733	1	0.714
5	1	14	0.933	1	0.928
6	2	12	0.8	0.5	0.846
7	1	11	0.733	1	0.071
8	2	12	0.8	0.5	0.846
9	2	7	0.467	0.5	0.461
10	2	12	0.8	0.5	0.846

Non-zero differences = 9, Wilcoxon statistic = 21, P > 0.05

Table 6.6. The effect of prey encounters on prey detection rate.

Prey detection rate (prey/s)

Experiment	1a		1b		1c	
Period	Initial	Final	Initial	Final	Initial	Final
1	0.038	0.035	0.148	0.074	0	0.066
2	0	0	0.294	0.255	0.197	0.427
3	0.121	0.114	0.059	0.169	0.036	0.071
4	0.143	0.129	0.187	0.238	0.048	0.252
5	0.488	0.465	0	0.253	0.081	0
6	0.118	0.129	0	0.255	0.041	0.180
7	0.033	0.168	0.167	0.174	0.025	0.042
8	0.176	0.635	0.173	0.425	0	0
9	0.032	0.072	0.326	0.119	0	0
10	0.064	0.199	0.117	0.339	0.091	0.102
Mean dif.	0.073		0.083		0.062	
t	1.57		1.61		2.07	
d.f.	9		9		9	
P	0.150		0.141		0.077	

Combined probability = -2 (-1.90 - 1.96 - 2.56)
= 12.84

d.f. = 6, P < 0.05

Initial and final prey detection rates were calculated from the first and last three encounters respectively.
Mean dif. = Mean difference between the final and initial rate.

Table 6.7. Comparison of corrected detection probabilities for prey types 1 and 2 in single and double prey experiments.

	Detection probability				
Experiment	Prey type 1	Prey type 2	MU	n	P
Single prey	0.633	0.566	43.5	10,10	>0.05
Two prey	0.642	0.259	21.5	10,10	**<0.05***
MU	48.5	24.5			
n	10,10	10,10			
P	>0.05	>0.05			

MU = Man Whitney U statistic

* Wilcoxon matched pairs test: W = 1, N(d) = 7, **P <0.05**.

respect to prey type 1 in the double prey experiment. Although this difference between the prey was also apparent in the single prey experiments, the discrepancy was not significant. Thus the ability to detect prey type 2 was affected by the presence of prey type 1. Furthermore, analysis of the search rate (as estimated by give-up time) indicates that there was no significant difference between experiments (Table 6.8). This shows that: firstly, the two prey types were equally cryptic (at least, compared between trials when they occurred separately); secondly, subjects did not search at a slower rate when searching for two prey types.

Search speed and prey detection

According to the search rate hypothesis Guilford and Dawkins (1987) predict that predators that initially overlook prey should reduce their search rate, thereby increasing their ability to detect prey. The results from experiment 1 have demonstrated that the probability of detecting both prey types was greatest for those subjects that searched the slowest (Fig. 6.3). Therefore the subjects that "learned to see" the prey should have slowed down their search rate and this should be reflected in the time taken to recognize the absence of prey (i.e. the give-up time), because this is directly dependent upon the search rate.

In order to test this prediction, the proportional improvement in each subject´s detection ability was calculated and related to their change in search rate. The proportional improvement in detection ability was calculated by dividing the total number of prey detected in the last four prey encounters by the sum of those detected in the first four and last four encounters. Similarly, for each subject the change in search rate was measured by dividing the give-up time for the first blank frame encountered by the sum of the give-up times for the first and last blank frames. The change in search rate was then taken as the independent variable and regresssed against the change in detection ability. Both proportions were transformed by arcsine transformation before regression. The data from Experiments 1a and 1b were combined because there was no apparent difference between prey in detection ability or give-up time when presented in separate trials (Tables 6.7 and 6.8). However, prey were treated separately in the analysis of Experiment 1c because prey 2 was

Table 6.8. The results of an analysis of variance comparing mean give-up times between experiments.

Source	Sum of squares	d.f.	Mean square	F	P
Experiment	61.58	2	30.8	1.24	>0.05
Error	672.25	27	24.9		
Total	733.8	29			

Experiment	1a	1b	1c
Mean give-up time (s)	6.33	9.79	7.57
Standard Error	0.821	1.55	2.09

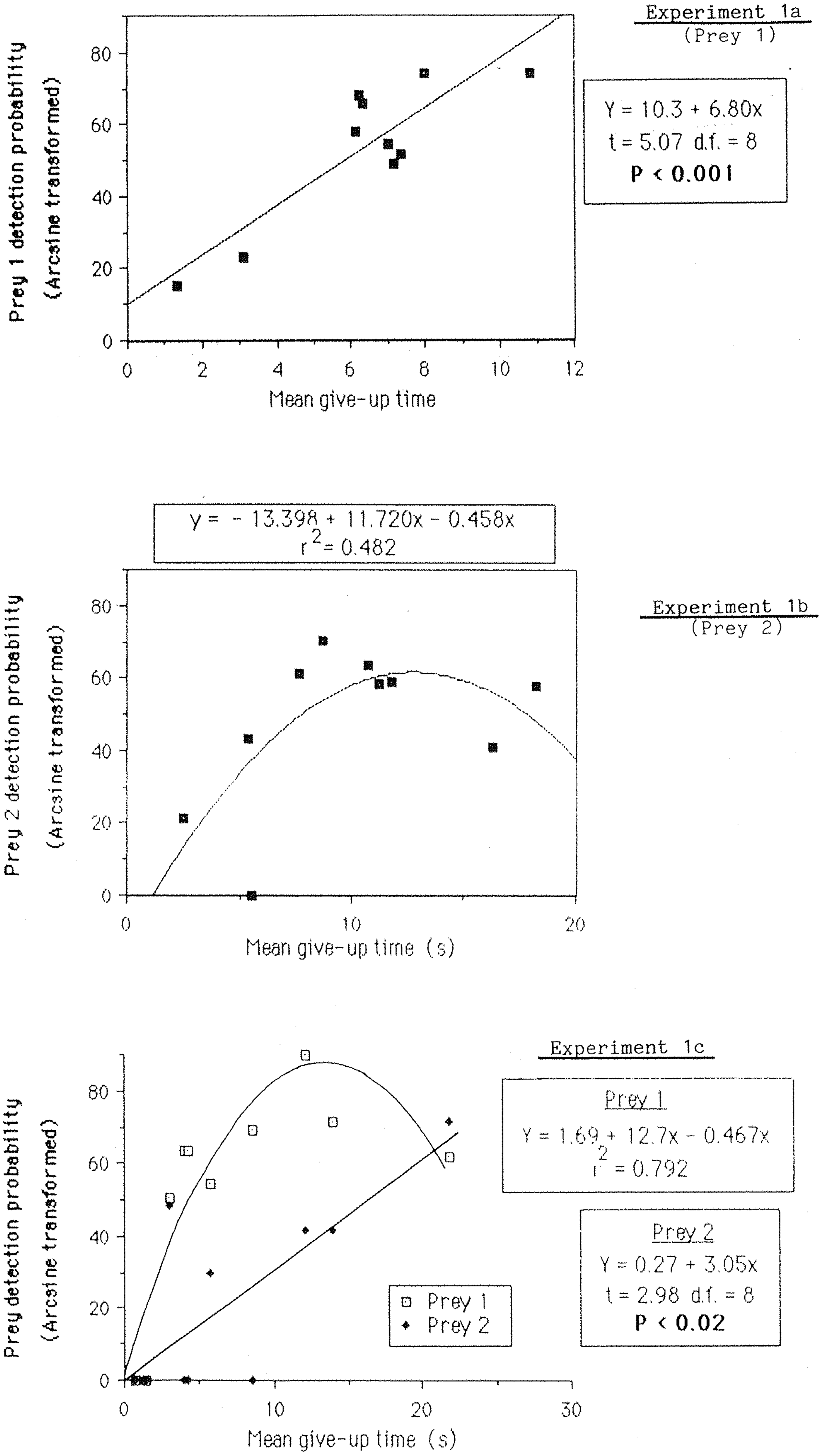


Fig. 6.3. The effect of mean give-up time on prey detection.

detected less often than prey 1 when presented in trials with both prey types. The results of the analyses are presented in Fig. 6.4. Clearly an increase in the ability to detect prey was associated with an increase in give-up time when the two prey types were presented separately. Furthermore this effect was statistically significant ($t = 2.19$, d.f. = 18, $P < 0.05$). This result indicates that the subjects did increase their ability to detect the prey by decreasing their search rate and therefore this supports the search rate hypothesis. However, in Experiment 1c, where subjects encountered both prey types, there was no significant association between changes in the ability to detect prey and changes in give-up time for either prey.

EXPERIMENT 2 RESULTS

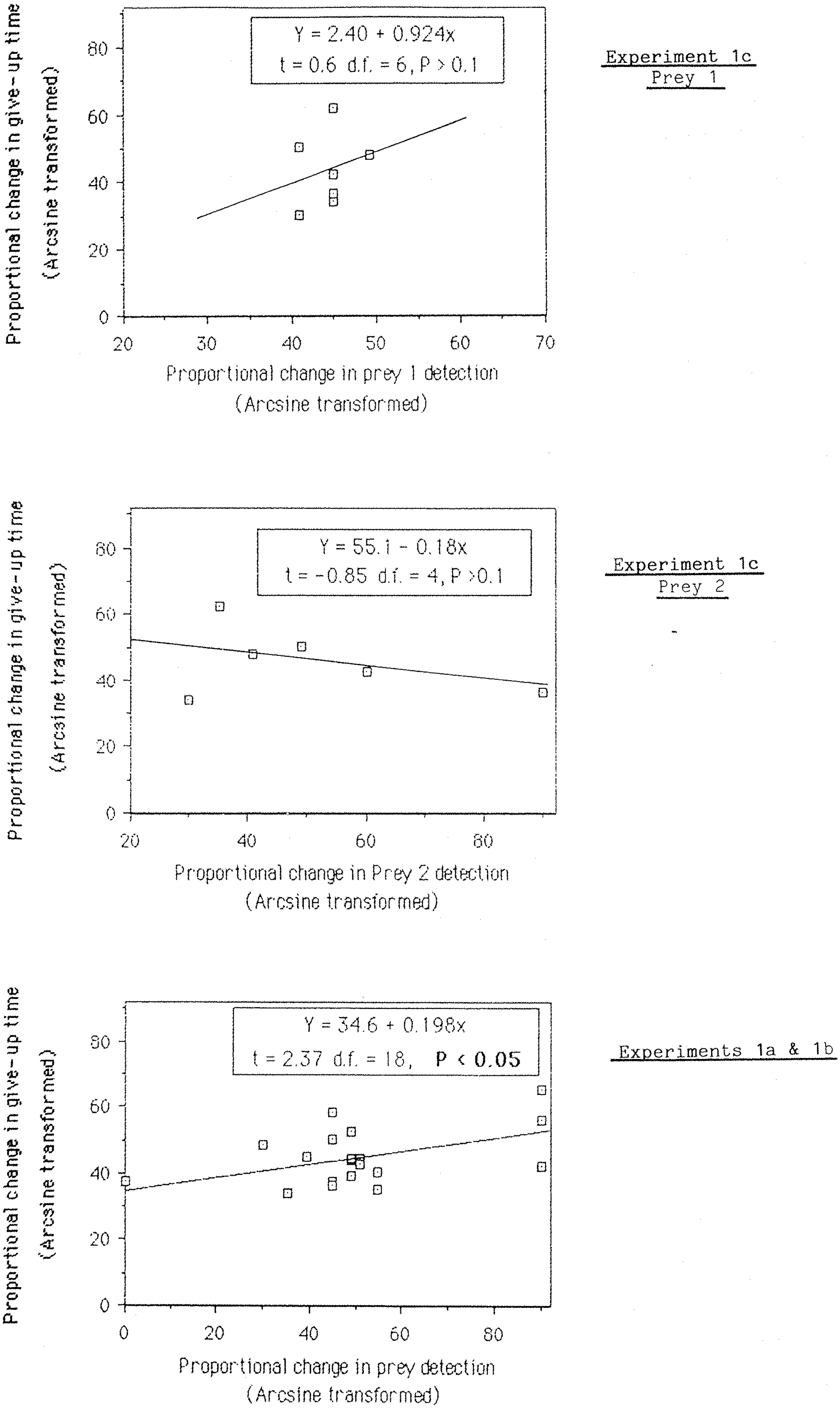
Each subject´s responses are summarised in Table 6.9 and 6.10.

The effect of successive prey encounters on detection ability

Figure 6.5 plots prey detection success (percentage detected and arcsine transformed) against prey encounter, for both prey types and at each frequency. Although 5 out of the 6 regressions indicate that detection success increased with encounter, in only one case (where Prey type 2 was most common) was this significant. Furthermore, 5 out of 6 positive regressions is not a significant departure from a random response (G-test for goodness of fit; $G = 2.69$, d.f. = 1, $P > 0.1$). However, in the trials where the prey were at equal frequencies, the potential for improving prey detection was severely limited, because the initial detection probabilities were very high. Clearly, this reduces the validity of the regression analysis for these particular trials. As the remaining trials showed positive slopes, this suggests that overall, there was some improvement in the ability to detect both prey types, particularly when common.

The effect of successive prey encounters on detection rate

As in the previous experiment the effect of encounters on the prey detection rate was tested by comparing the rate over the first three encounters with the final rate over the last three



<u>Experiment 1c</u>
<u>Prey 1</u>

<u>Experiment 1c</u>
<u>Prey 2</u>

<u>Experiments 1a & 1b</u>

Fig. 6.4. The relationship between changes in prey detection and change in give-up time.

Table 6.9. Summary of subject responses in Experiment 2.

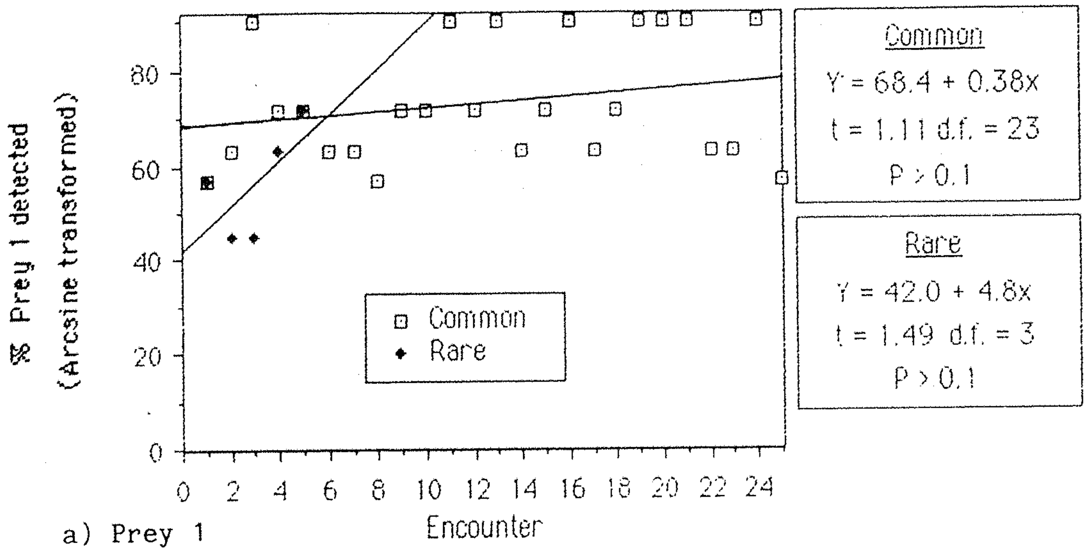
Subject			Response											
	P1	P2	1	2	0	+1	+2	-1	-2	?1	?2	DT1	DT2	DT0
1	5	25	5	25	13	0	0	2	0	0	0	3.32	2.61	12.1
2	5	25	4	21	13	1	4	2	0	0	0	2.50	1.77	4.63
3	5	25	1	10	6	3	11	5	4	4	1	2.52	2.09	1.37
4	5	25	4	25	14	1	0	1	0	0	0	3.45	1.94	4.15
5	5	25	2	21	9	2	3	6	0	1	1	6.12	3.42	9.60
6	5	25	1	6	14	4	19	1	0	0	0	3.29	5.11	9.61
7	5	25	4	22	15	1	3	0	0	0	0	3.43	3.06	6.09
8	5	25	4	23	14	1	2	1	0	0	0	5.30	3.81	9.33
9	5	25	5	25	13	0	0	2	0	0	0	2.56	6.75	15.7
10	5	25	3	22	13	2	2	2	0	0	1	2.85	5.96	9.25
Mean												**3.53**	**3.65**	**8.18**
S.E.												0.39	0.55	1.32
11	15	15	14	15	15	1	0	0	0	0	0	3.06	3.11	7.39
12	15	15	14	13	15	1	2	0	0	0	0	2.82	2.25	8.03
13	15	15	15	14	15	0	1	0	0	0	0	2.11	2.35	5.47
14	15	15	15	15	15	0	0	0	0	0	0	3.06	4.25	10.7
15	15	15	15	14	15	0	1	0	0	0	0	4.29	4.91	26.5
16	15	15	14	14	12	1	0	3	0	1	0	10.1	7.73	18.2
17	15	15	14	15	14	1	0	1	0	0	0	8.01	5.08	25.2
18	15	15	10	15	14	5	0	1	0	0	0	2.06	1.93	4.26
19	15	15	14	15	15	1	0	0	0	0	0	3.75	3.09	8.50
20	15	15	15	15	15	0	0	0	0	0	0	3.79	2.77	7.80
Mean												**4.30**	**3.75**	**12.2**
S.E.												0.84	0.56	2.57
21	25	5	21	4	14	4	1	0	1	0	0	2.38	3.18	4.67
22	25	5	23	3	15	2	2	0	0	0	0	3.91	4.78	10.3
23	25	5	24	4	15	1	0	0	0	0	0	3.75	2.69	9.30
24	25	5	21	0	15	4	5	0	0	0	0	3.98	-	9.01
25	25	5	17	2	15	7	3	0	0	0	1	5.42	7.03	8.84
26	25	5	24	3	15	1	0	0	0	2	0	3.74	9.14	9.58
27	25	5	19	2	13	5	3	2	0	0	1	3.17	1.33	6.78
28	25	5	24	4	0	0	0	7	8	1	1	2.26	2.67	-
29	25	5	21	0	12	2	5	0	3	0	2	5.81	-	12.0
30	25	5	25	4	15	0	1	0	0	0	0	5.75	10.3	12.0
Mean												**4.02**	**5.15**	**9.17**
S.E.												0.41	1.17	0.78

P1 = Number of Prey 1 presented
P2 = Number of Prey 2 presented
1 = Prey 1 present and detected
2 = Prey 2 present and detected
0 = Prey absent and correct answer
+1 = Prey 1 present and undetected
+2 = Prey 2 present and undetected
-1 = Prey absent and key 1 pressed
-2 = Prey absent and key 2 pressed
?1 = Prey 2 present and key 1 pressed
?2 = Prey 1 present and key 2 pressed
DT1 = Mean Prey 1 detection time.
DT2 = Mean Prey 2 detection time.
DT0 = Mean prey absence recognition time.

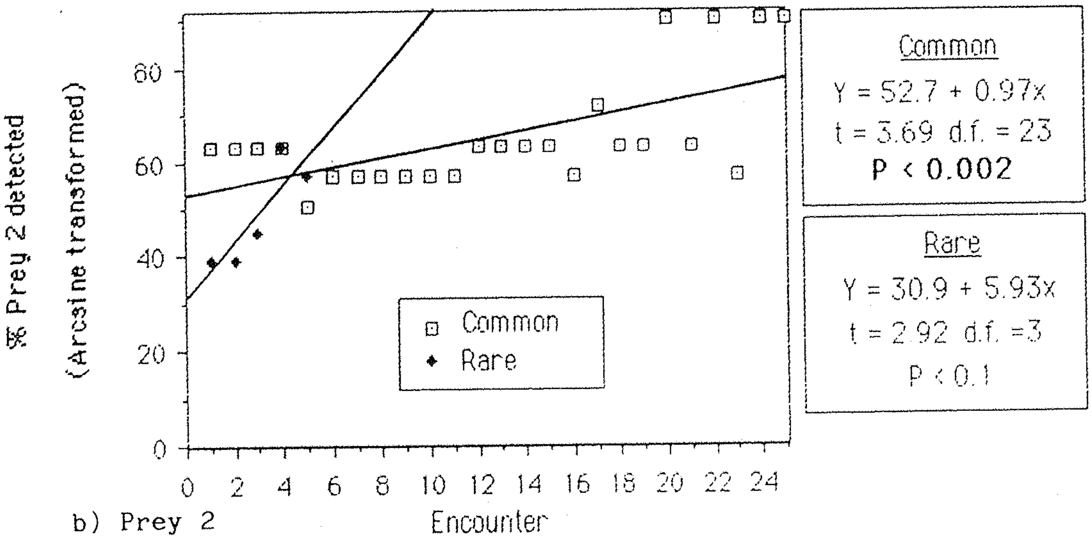
Table 6.10. Summary of detection probability and prey selection in Experiment 2.

Subject				Response		
	P1	P2	PD1	PD2	Betalt	PD0
1	5	25	1	1	45.0	0.867
2	5	25	0.769	0.84	43.7	0.867
3	5	25	0	0.182	0	0.4
4	5	25	0.786	1	41.5	0.933
5	5	25	0	0.84	0	0.6
6	5	25	0.143	0.24	37.7	0.933
7	5	25	0.8	0.88	43.6	1
8	5	25	0.786	0.92	42.7	0.933
9	5	25	1	1	45.0	0.867
10	5	25	0.538	0.88	38.0	0.867
Mean			**0.582**	**0.778**	**33.7**	**0.679**
S.E.			0.124	0.097	5.68	0.044
11	15	15	0.933	1	44.0	1
12	15	15	0.933	0.867	46.0	1
13	15	15	1	0.933	46.0	1
14	15	15	1	1	45.0	1
15	15	15	1	0.933	46.0	1
16	15	15	0.917	0.933	44.7	0.8
17	15	15	0.928	1	43.9	0.933
18	15	15	0.643	1	38.7	0.933
19	15	15	0.933	1	44.0	1
20	15	15	1	1	45.0	1
Mean			**0.929**	**0.967**	**44.3**	**0.843**
S.E.			0.034	0.015	0.68	0.030
21	25	5	0.84	0.786	45.9	0.933
22	25	5	0.92	0.6	51.1	1
23	25	5	0.96	0.8	47.6	1
24	25	5	0.84	0	90.0	1
25	25	5	0.68	0.4	52.5	1
26	25	5	0.96	0.6	51.7	1
27	25	5	0.723	0.4	53.3	0.867
28	25	5	0.925	0.571	51.8	0
29	25	5	0.84	0	90.0	0.8
30	25	5	1	0.8	48.2	1
Mean			**0.869**	**0.496**	**58.2**	**0.747**
S.E.			0.033	0.095	5.35	0.089

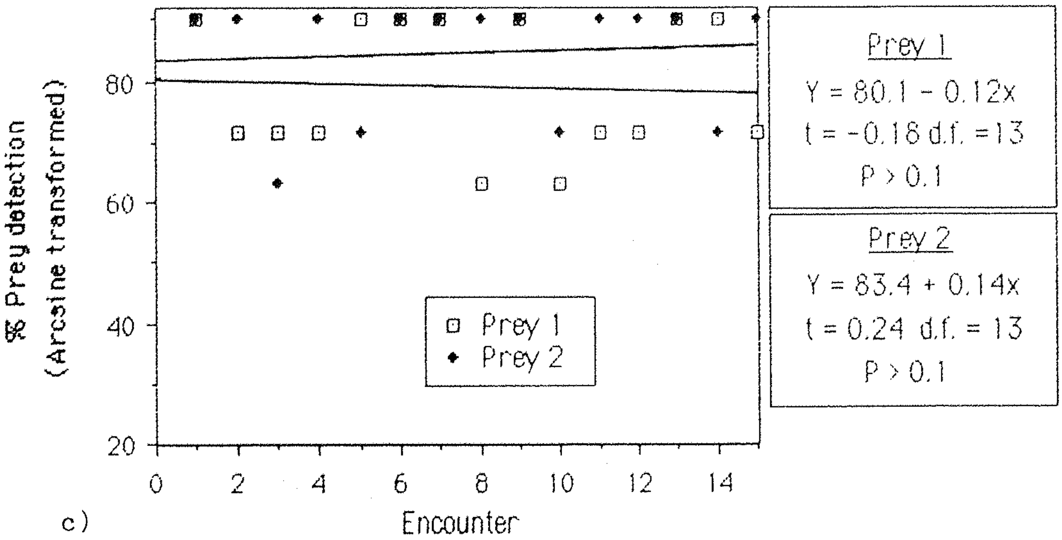
P1 = Number of Prey 1 presented
P2 = Number of Prey 2 presented
PD1 = Corrected probability of prey 1 detection (see text)
PD2 = Corrected probability of prey 2 detection (see text)
PD0 = Probability of recognizing prey absence
Betalt = Manly´s (1973) Beta selection coefficient (for experiments with prey replacement) for Prey 1 (arcsine transformed).



a) Prey 1



b) Prey 2



c)

Fig. 6.5. The effect of encounters with prey on prey detection, in Experiment 2. a) and b) are trials with unequal prey frequencies. c) Prey 1 and 2 in equal frequency.

encounters, for each subject. Table 6.11 shows that for both prey and at each frequency, the final detection rate was higher than the initial rate and these differences were statistically significant in three out of the four cases. Although this was not significant in the trials when Prey 2 was common, overall the combined probabilities from the four tests indicate, that there was a highly significant increase in prey detection rate over the course of each trial.

Search speed and prey detection

The effect of variation between subjects in mean give-up time on their ability to detect prey was investigated by regression analysis, on both prey types and at each frequency. It is clear from Fig 6.6 that there was no significant effect for either prey at any frequency. Furthermore, there was no consistent trend in the slope of the regressions. These results indicate that the subjects did not increase their ability to detect a prey item by searching for a longer time. Thus, if give-up time reflects the rate of search, then these results also suggest that this had little effect on detection ability. Therefore, it is unlikely that the search rate hypothesis could apply to this experiment, because there appears to be no advantage in varying search speed within the range examined. To test this, the proportional improvement in each subject´s detection ability (with the two prey types treated as one) was compared with the proportional change in give-up time, as in the first experiment. The set of trials with prey at equal frequencies was not analysed, because only two subjects showed any change in detection ability between the first and last three encounters. Fig 6.7 presents the results of this analysis. Where Prey 1 was rare there was very little variation in the proportional change in prey detection. This restricted spread of data points along the independent variable axis makes the validity of the regression questionable. However, there appears to be no correlation between change in prey detection and give-up time. Where Prey 2 was rare however, the improvement in subjects ability to detect both prey types was associated with a decrease in give-up time and this was statistically significant. This suggests that in this case subjects did modify their search rates and thereby increased their ability to detect the prey.

Table 6.11. The effect of prey encounters on prey detection rate.

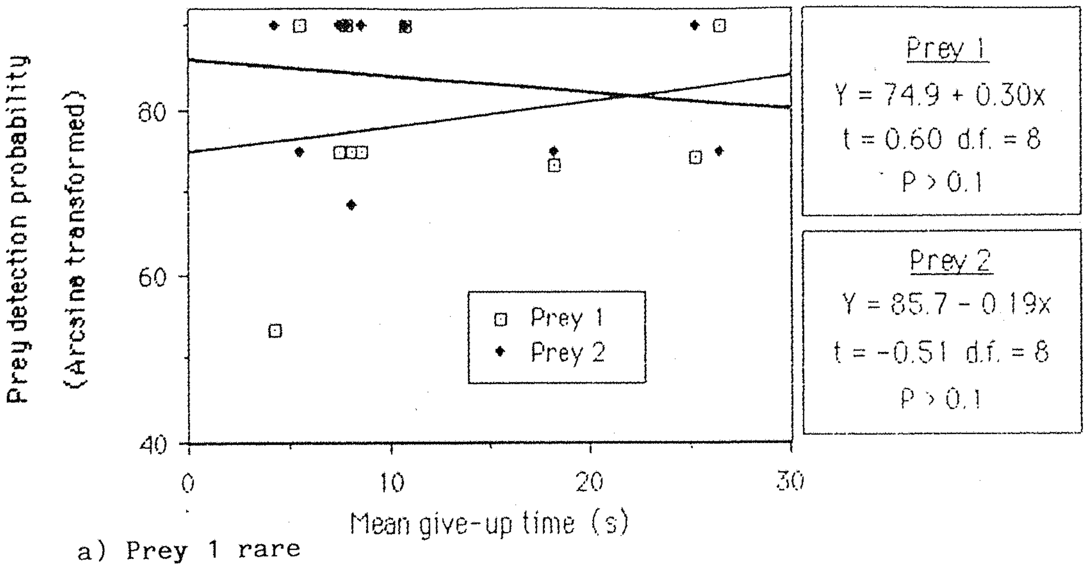
	Prey detection rate (prey/s)							
P1:P2	5:25		15:15				25:5	
Prey	2		1		2		1	
Period	I	F	I	F	I	F	I	F
1	0.224	0.108	0.295	0.336	0.223	0.382	0.371	0.785
2	0.171	0.240	0.127	0.416	0.163	0.439	0.416	0.655
3	0.173	0.235	0.310	0.469	0.220	0.263	0.484	0.306
4	0.310	0.402	0.303	0.250	0.101	0.470	0.486	0.857
5	0.084	0.043	0.143	0.414	0.081	0.513	0.143	0.155
6	0.217	0.441	0.041	0.112	0.026	0.157	0	0.322
7	0.243	0.337	0.057	0.226	0.110	0.381	0.206	0.451
8	0.502	0.255	0.204	0.544	0.518	0.519	0.196	0.243
9	0.079	0.120	0.217	0.225	0.266	0.568	0.059	0.374
10	0.104	0.304	0.214	0.315	0.376	0.403	0.023	0.223
Mean dif.	0.038		0.130		0.201		0.20	
t	0.855		3.40		4.22		3.39	
P	0.414		**0.0078**		**0.0022**		**0.0079**	

There were 9 degrees of freedom for each paired t-test.

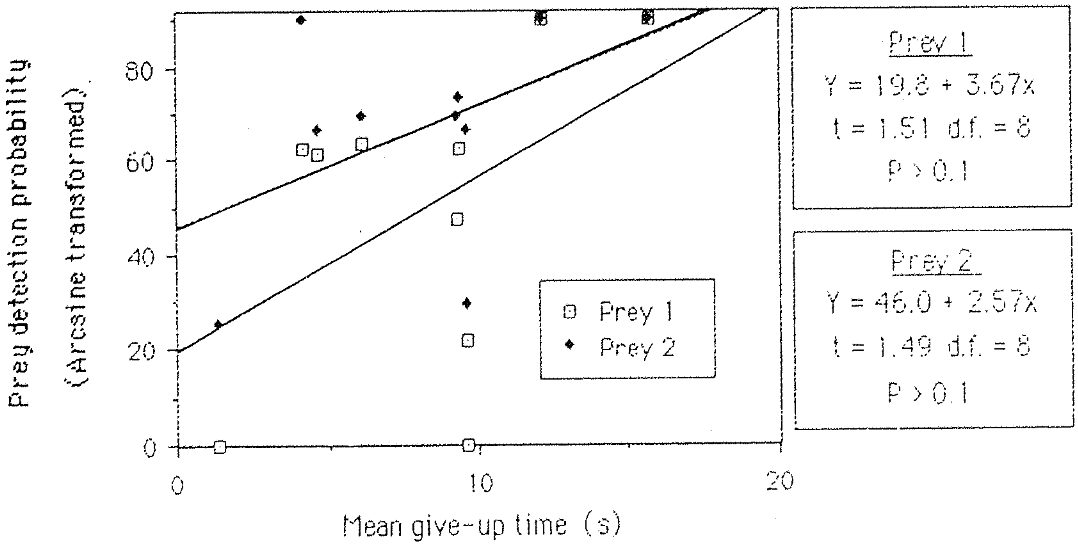
Combined probability = −2 (−0.88 −4.85 −6.12 −4.84)
= 33.38

d.f. = 8 **P < 0.001**

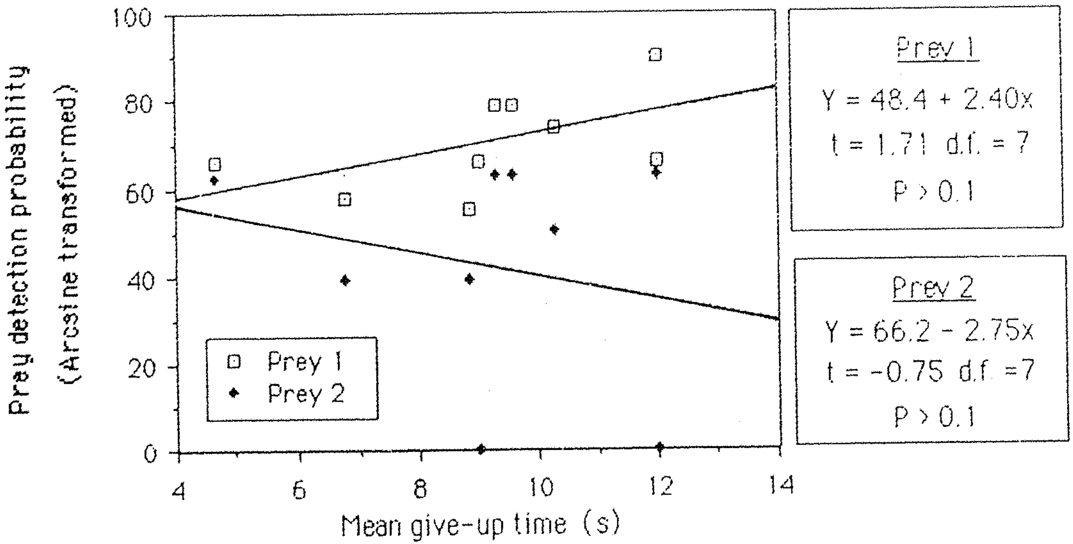
Period: I = Initial (first three encounters), F = Final (last three encounters).
Mean dif. = Mean difference between final and initial rate.



a) Prey 1 rare

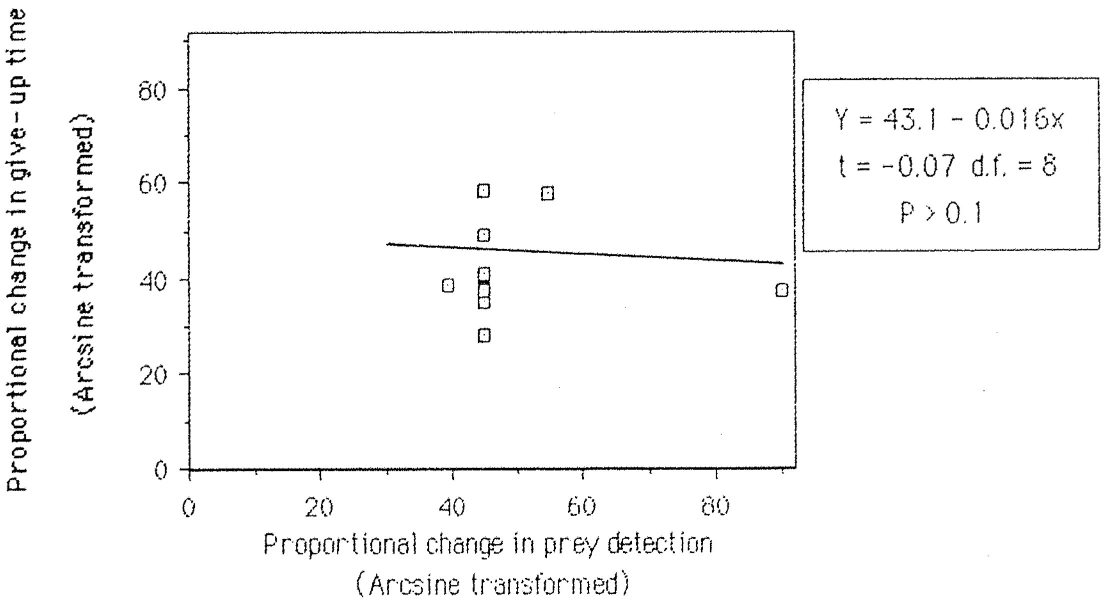


b) Prey at equal frequency

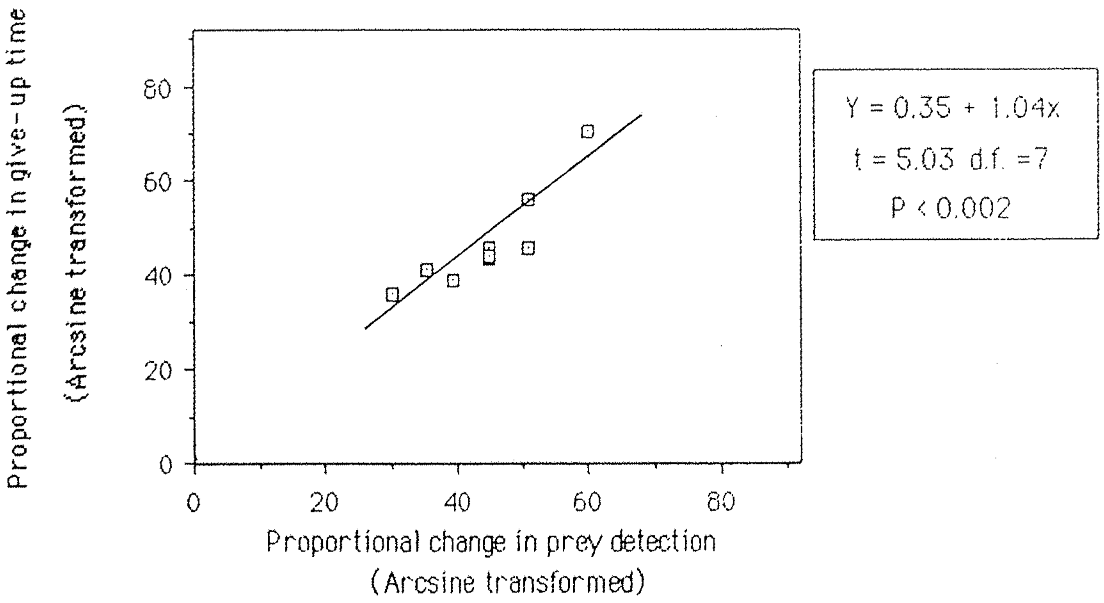


c) Prey 2 rare

Fig. 6.6. The effect of mean give-up time on prey detection.



a) Prey 1 rare



b) Prey 2 rare

Fig. 6.7. The relationship between changes in prey detection and change in give-up time.

The effect of prey frequency on detection ability.

The corrected detection probability for each prey at each frequency, together with the probability of detecting the absence of prey, is presented in Fig. 6.8. For both prey, the lowest detection probability occurred when the prey was rare, and the highest when the two prey types occurred at equal frequencies. Furthermore, there appears to be no difference between the prey types. The results of a two-way analysis of variance (on arcsine transformed values) confirmed that there were significant differences in detection probability at different prey frequencies, there was no effect of prey type and no interaction between prey type and prey frequency (Table 6.12). Although the probability of detecting the absence of prey appears to follow the same trend as the detection of prey, the differences between 'blanks' from the trials of different prey frequency were not significant (one-way ANOVA; $F = 1.88$, d.f. $= 2,27$, $P > 0.1$). The effect of prey frequency on detection probability was further analysed by one-way analysis of variance after combination of the data from both prey. Table 6.13 indicates that the detection probabilities were significantly different for each pairwise frequency comparison.

The effect of prey frequency on give-up time

The results of a one-way analysis of variance (Table 6.14) show that there were no significant differences between the mean give-up times at different prey frequencies. Therefore, because the give-up time (i.e. the time taken to decide that a prey item is absent) is directly related to search rate, it appears that prey frequency did not affect the rate of search.

The effect of prey frequency on prey selection

There was no difference between the two prey types in their conspicuousness (Table 6.12) and therefore we should not expect apostatic selection as a result of search rate optimization (Staddon & Gendron 1983). Furthermore, Guilford & Dawkins (1987) predict that if apostatic selection occurs, then this is in itself evidence for the acquisition of a search image for the common prey. To test for apostatic selection, for each subject Manly's

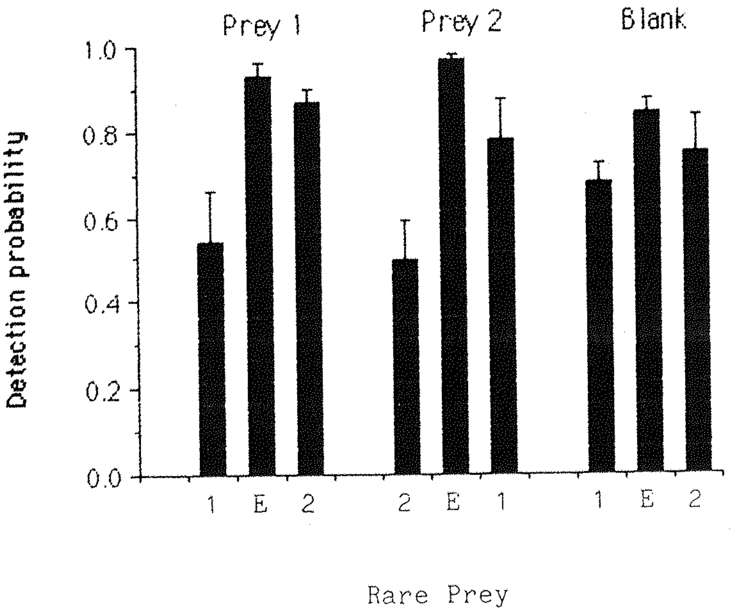


Fig. 6.8. The effect of prey type and frequency on prey detection and recognition of prey absence. Prey frequency codes are: 1 = Prey 1 rare, 2 = Prey 2 rare, E = both prey at equal frequencies. Standard errors are indicated by the vertical bars.

Table 6.12. Two-way analysis of variance on the effects of prey frequency and prey type on detection probability.

Source	Sum of squares	d.f.	Mean square	F	P
Prey	82.1	1	82.1	0.198	0.342
Frequency	12730	2	6365	15.3	**<0.001**
Interaction	426	2	213	0.514	0.399
Error	22385	54	414.5		
Total	35623	59	603.7		

N.B. Detection probabilities were arcsine transformed for this analysis.

Table 6.13. One-way analysis of variance on the effects of prey frequency on the probability of detection.

	P1:P2 ratio	Mean detection probability	S.E.
A	1:5	0.515	0.012
B	1:1	0.975	0.0016
C	5:1	0.870	0.0047

Pairwise comparisons

A/B F = 27.5, d.f. = 1,38, P <0.001

A/C F = 9.67, d.f. = 1,38, P **<0.01**

C/B F = 7.03, d.f. = 1,38, P **<0.01**

(Data were arcsine transformed for the analysis).

Table 6.14. Results of an analysis of variance on the effects of prey frequency on give-up time.

Source	Sum of squares	d.f.	Mean square	F	P
Frequenncy	87.46	2	43.73	1.43	0.258
Error	795.3	26	30.59		
Total	882.7	28			

(1973) Beta selection coefficient was calculated for prey type 1 and transformed by arcsine transformation (Table 6.10). These values were then regressed against Prey 1 frequency.

Selection on Prey 1 increased with Prey 1 frequency (Fig. 6.9) and the deviation of the regression slope from zero is highly significant (t = 3.89, d.f. = 28, $P < 0.001$). Although this slope is markedly affected by some outlying points at each frequency extreme, the slope remains positive and highly significant if these points are excluded from the analysis ($Y = 39.39 + 12.18x$, t = 6.07, d.f. = 24, $P < 0.001$). The selection coefficient for Prey 1 when the prey frequencies were equal did not differ significantly from 45, i.e. the value expected in the absence of selection ($Beta_{(transformed)} = 44.3$, t = 0.987, d.f. = 9, $P > 0.1$). Furthermore, the regression line crosses the line of no selection. Therefore, these results clearly indicate that the human subjects searched in an apostatic manner for the prey images, when presented in sequence.

The relationship between apostatic selection and give-up time

Apostatic selection could be an adaptive mechanism whereby subjects that concentrate on the common form of prey search faster than those who search for both. To test this, regression analysis was carried out on the effect of each subject's selection on their overall search rate (as estimated by give-up time). Fig 6.10 shows the results of this analysis for the two sets of trials where prey frequencies were unequal. In neither case was there a significant relationship between selection and give-up time. Furthermore, if apostatic selection leads to an increase in search rate, a negative slope would be expected when Prey 1 was rare, because, at this frequency an increase in apostatic selection is indicated by a decrease in Beta. This was not the case. Therefore, this analysis indicates that apostatic selection was not associated with faster searching.

The effect of selection on overall detection rate

Although apostatic selection did not appear to be related to search rate, it could still be adaptive if it increases the overall detection rate, by increasing the subject's ability to

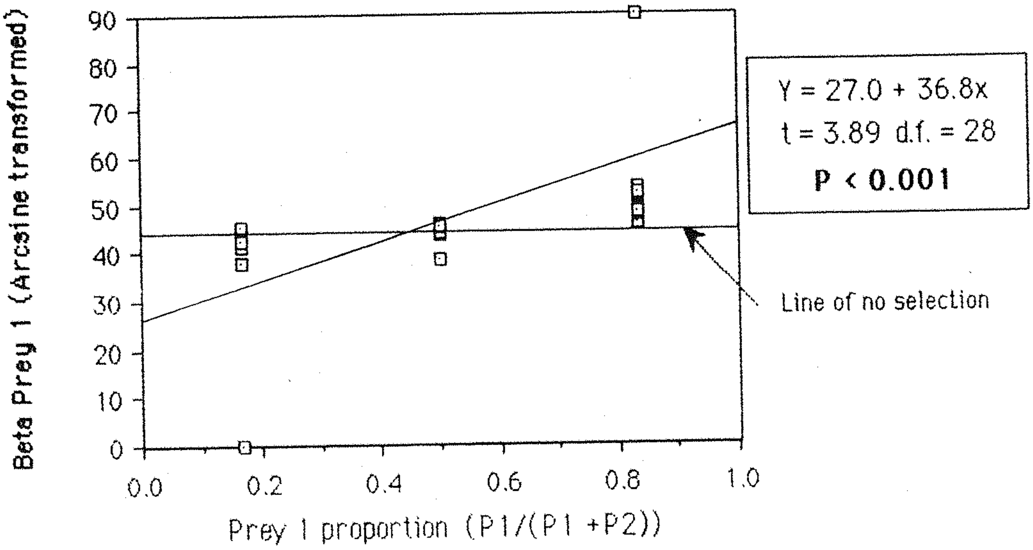


Fig. 6.9. The effect of prey frequency on selection.

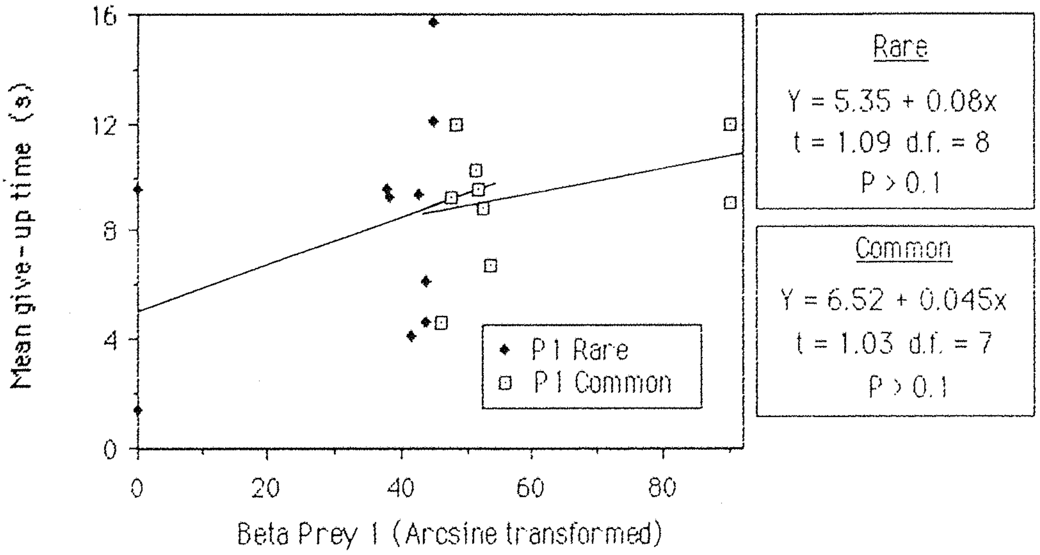


Fig. 6.10. The effect of selection on mean give-up time.

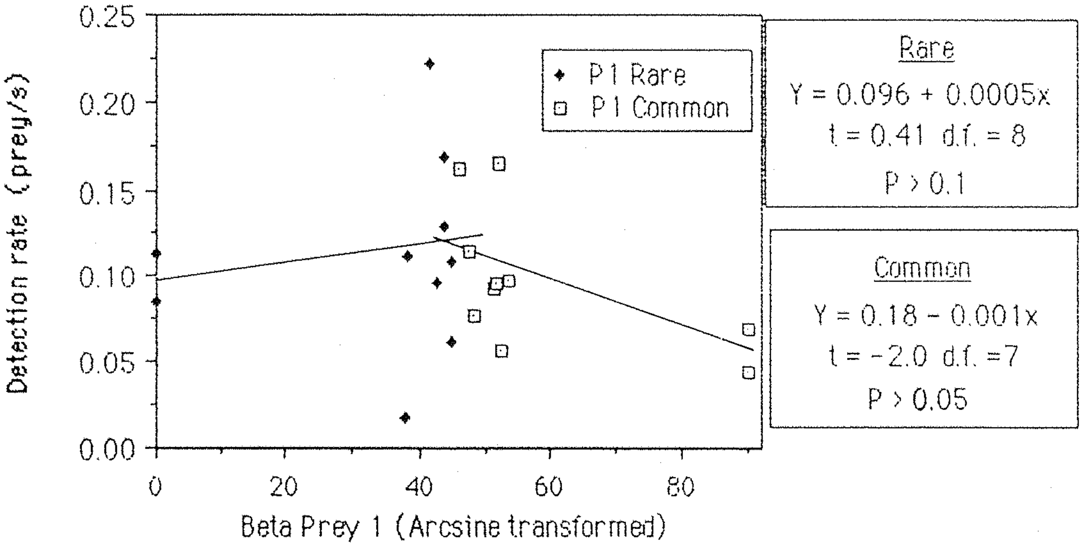


Fig. 6.11. The effect of selection on overall detection rate.

detect prey. This was tested by regressing Prey 1 selection (as measured by Beta) against overall prey detection rate, for each subject, in the two sets of trials with unequal prey frequencies. The results of the analysis are presented in Fig. 6.11. Neither regression was significant. Therefore subjects that selected in an apostatic manner did not increase their overall prey detection rate. This provides further evidence that apostatic selection was not an adaptive optimal foraging strategy in this particular experiment.

DISCUSSION

The aim of these experiments was to examine the behaviour of humans searching for cryptic prey images, and to test the search image and search rate hypotheses, as explanations for any perceived improvement in the subjects rate of prey detection.

The results of both experiments showed that although generally the subjects did not increase the proportion of prey detected over the course of each trial, they did increase their overall rate of prey detection. These results are similar to those obtained in earlier experiments using birds, in which prey detection rate was shown to increase with experience (Dawkins 1971a; Lawrence 1985a,b; Gendron 1986). Pietrewicz & Kamil (1979) demonstrated that the probability of blue jays detecting the presence of a projected image of a cryptic moth increased with increased encounters. However, the results of all these previous experiments, which claimed to provide evidence for search image development, can be equally well explained by the search rate hypothesis (Guilford & Dawkins 1987). In order to distinguish between the two hypotheses as explanations for my results I have tested the predictions of Guilford & Dawkins (1987) relating to the differences between the mechanisms.

Search image interference.

Guilford & Dawkins (1987) state that if a search image is formed for a prey, then this will be specific to that prey and will interfere with the ability to detect other prey. Alternatively, the search rate hypothesis predicts that a predator that learns to detect prey by slowing down its search rate will be equally able to detect other equally cryptic prey. The results from Experiment 1 showed that prey detection probability was not significantly lower in trials with both prey types, compared with trials with one prey type. Additionally, in Experiment 2 the highest detection probability for both prey occurred when the two prey types were at equal frequencies. Both results suggest that there was no additional cost to searching for two types of prey simultaneously, when present in equal frequencies. Therefore there was no evidence that search image interference occurred in these particular circumstances.

The prediction of interference between search images is based upon the initial ideas of Tinbergen (1960), where he suggested that some form of perceptual filter was involved. The acquisition of a such a filter would block visual 'noise' and allow the predator to concentrate on the specific pattern of the target prey. Consequently, the predator's ability to detect other forms of prey is actively reduced. Tinbergen also suggested that the development of a search image is dependent upon the rate of encounter with the particular prey item. Search images will only be formed for prey which are encountered often, because only these will provide sufficient opportunities for the predator to learn to recognize the prey and distinguish it from the background. Thus the proximate causes for search image interference are: firstly, if only one or a small number of search images can be formed at any one time; secondly, if alternative prey are not encountered sufficiently often for search images to be formed. However, Tinbergen's (1960) ideas were not supported by any detailed behavioural evidence. Furthermore, to date the underlying perceptual mechanism of the search image is very poorly understood, although some form of selective attention (see Johnston & Dark 1986 for review) is thought to be involved (Croze 1970; Krebs 1973; Bond 1983; Lawrence & Allen 1983; Gendron 1986).

At present there is no evidence to suggest that if search images exist they are likely to be restricted to one or a very small sub-set of prey. Indeed, Blough (1979) found that in experiments using luminous images as prey on a large display field, the search rate of pigeons was unaffected when the number of types of image was increased from one to two. Although Teichner and Krebs (1974) and Schneider and Shiffrin (1977) found that humans searching visually for targets took longer to respond as the number of potential targets increased, the latter study showed that the response was not linear, but approximated to a $\log_2$ function of the number of targets. Furthermore Schneider & Shiffrin (1977) found that this effect decreased rapidly with experience, until the subjects were equally efficient at searching for the increased target set. Similar results were obtained by Neisser (1964) in experiments with humans searching for letters amongst a group of random non-target letters. Although these studies did not claim to involve search images, and the results of experiments with humans as ´predators´ and letters as ´prey´ should be interpreted with care regarding their relevance to animal searching behaviour, they have important implications. Combined with the study by Blough (1979), they suggest that both humans and pigeons can adopt automatic detection processes that enable parrallel and simultaneous processing of several visual stimuli. Furthermore, selective attention is no longer assumed to be limited by capacity. Instead, an active control process is thought to modulate the flow of information to memory and attenuate some input (Keele & Neill 1978). Thus, the perceptual filter suggested by Tinbergen (1960) may be represented by the control processes, whereby stimuli for a target prey item (for which a search image has been formed) are allowed to proceed, whilst other visual ´noise´ stimuli are rejected. The search image therefore can be regarded as the presetting of the control process on the basis of expected information. Present information therefore suggests that a predator is unlikely to be limited to having one or two search images at any one time. Furthermore, the addition of each search image will only result in a small and temporary increase in visual processing time.

Search image interference is also predicted to occur when some prey are only rarely encountered, and the predator has formed a search image for other, commonly encountered prey. Thus the detection of the rare prey is actively inhibited. There is no information available on the number and frequency of encounters needed to promote search image development (Gendron 1987). Therefore, in experiments where prey are encountered at different rates, it is difficult to predict for which prey search images will be developed, and whether search image interference will occur. Although the demonstration of interference in such experiments provides evidence for search image development, the absence of such an effect does not refute the acquisition of a search image. However, there was a clear indication in Experiment 2 that the ability to detect both prey types was significantly reduced when they were rare. The results thus support the predictions of Guilford & Dawkins (1987): there is strong evidence for detection interference and therefore search image development for the common prey.

A complicating factor concerning search image inteference is the specificity of the image. Although conventionally, a search image is regarded as being specific to one type of prey (Tinbergen 1960), it is conceivable that they might encompass the recognition of characteristics common to several similar prey. Indeed Croze (1970) found that wild carrion crows that learnt to detect cryptic red shells would also investigate shells with similar but not identical colours. Although his experiments did not conclusively demonstrate the development of search images, it does show that predators may use general cues to detect prey items. If this is the case with search images, then this may eliminate interference within groups of similar prey species, irrespective of their encounter rates. Thus, if search images can incorporate the recognition of characters shared by a set of prey, then rare prey that are visually distinct from common prey will be at a selective advantage.

Search rate modification

The search rate hypothesis (Guilford & Dawkins 1987) predicts that subjects that learn to detect cryptic prey should slow down their search rate. In the experiments described in this chapter it was not possible to measure the search rate directly. Instead, it was estimated by measuring the time taken to recognize the absence of prey in each frame. Detection time cannot be used as a measure of search rate as it is not independent from the give-up time, because the upper limit of detection time is restricted by the maximum time a subject will spend searching for a prey time. Additionally, the detection time is highly variable, because it is dependent upon the chance positioning of the prey item on the background, and thus there is variation in prey conspicuousness between frames. Another problem is that if subjects develop search images as well as modifying their search rate, then the increased ability to detect prey might allow an increase in search rate, thereby offsetting any decrease.

The experiments showed that in some cases, increases in the ability to detect prey were significantly associated with decreases in search rate (i.e. give-up time). Thus there is some evidence to support the search rate hypothesis, although its generality remains unclear.

Apostatic selection

There are many mechanisms that can give rise to apostatic selection (Murdoch, Avery & Smyth 1975; Greenwood 1984). Of these, only those that involve some effect of searching are relevant, because others depend on properties that the 'prey' did not have, such as differences between the prey types in spatial distribution and profitability. Apostatic selection may be caused by searching behaviour through the minimisation of searching costs (Greenwood 1984), search image formation (Tinbergen 1960; Clarke 1962a; Guilford & Dawkins 1987), or search rate modification (Gendron & Staddon 1983, Greenwood 1984). However, the latter is only applicable where prey are not equally cryptic. Furthermore the most cryptic type of prey will never be eaten in excess, even when it is most common. Therefore search rate modification does not explain these results, because the prey appeared to be equally cryptic and both prey were detected proportionately more often when they were common. These results also show that there does not appear to be a cost to searching for two types of prey simultaneously and therefore, the most likely basis for the observed apostatic selection is that it was caused by the development of a search image for the common prey, which interfered with the detection of the rarer prey.

It is generally assumed that the adaptive significance of search image development is that it increases the hunting efficiency of the predator by maximising the prey detection rate (Tinbergen 1960; Krebs 1973). However, the analysis failed to find any association between the degree of selection and searching efficiency. This suggests that in these particular circumstances apostatic selection may be a constraint rather than an adaptive foraging strategy. Similarly, the rate of prey detection was not found to be significantly associated with the degree of apostatic selection in previous experiments with humans selecting prey images on a VDU (see Chapter 5 and Tucker & Allen 1988). However, Weale, Allen & Tucker (1988) did find such an effect in similar experiments, but with four prey types simultaneously available.

Irrespective of the underlying mechanism, the demonstration of apostatic selection in Experiment 2 is the first evidence that predators may select dispersed prey in an apostatic manner. All previous experiments have used populations of prey that were at sufficiently high densities that a predator was constantly provided with a number of prey within its field of view at any one time (see Allen 1988 for review). These experiments are probably more realistic in representing the distribution of natural prey and their mode of encounter for most predators.

CHAPTER 7

GENERAL DISCUSSION

The preceeding chapters of this thesis contain extensive and detailed discusson of the experimental results in relation to other studies. Therefore, this chapter will be limited to an extended summary and a brief discussion of potential future research.

CONCLUSIONS FROM THE STUDY

Chapter 1 reviewed the current state of knowledge on visual predation of polymorphic prey, apostatic selection and it´s causal mechanism, and identified several areas where more information is needed. In particular, little information is available on the generality of visual selection by predators, the factors that affect the direction, degree and timing of such selection, whether apostatic selection occurs on natural polymorphic prey and what is it´s causal mechanism. Therefore in an attempt to fill some of these gaps in our knowledge, this study aimed to:

(1) study a predator-polymorphic prey system and attempt to establish whether predators exert visual selection on these prey and if so, which factors affect the degree and direction of selection,

(2) establish whether predators can exert apostatic selection on natural polymorphic prey, by laboratory and large scale field experiments,

(3) establish the behavioural mechanism(s) underlying apostatic selection in visually hunting predators.

The study of song thrush predation on *Cepaea hortensis* and other polymorphic landsnails, at Rogate, provided some evidence of visual selection. However, heterogeneity between anvil sites restricted the investigation of selection to *Cepaea hortensis* and prevented the assessment of the effect of frequency-dependent selection by manipulation of morph frequencies. The snail population was found to be too large and heterogeneous for such a large scale field experiment to work at this site. Predation occurred during two periods in the year; mid-winter and mid-summer. Furthermore, detailed measurements of predation rates and meteorological parameters confirmed earlier suggestions that snail predation by song thrushes is restricted to periods of extreme cold or dry weather (Goodhart 1958; Davies & Snow 1965).

Investigation of morph predation during one winter period revealed that five-banded yellow (Y12345) morphs were at a selective advantage. The most likely explanation for this was that the song thrushes were exerting visual selection on the basis of the difference in degree of crypsis between the morphs. As far as I am aware this is the first demonstration of visual selection by song thrushes on populations of *Cepaea* during the winter. Furthermore it refutes the suggestion by Lamotte (1951) that song thrush predation during the winter is non-selective because the snails are buried and therefore visual cues cannot be used for their detection.

Five-banded yellow morphs were also at a selective advantage in both summer predation periods as were yellow unbanded, whilst morphs with fused bands were at a selective disadvantage. Although these results generally agree with the earlier studies by Wolda (1963) and Carter (1968a), unlike these studies no change in selection was observed over the summer predation periods. These results can also be explained on the basis of visual selection for crypsis. However, the interpretation of what is cryptic to a thrush in a complex background of fully grown vegetation is fraught with difficulties. Therefore, this demonstration of selection should not be equated with a demonstration of visual selection (see Clarke *et al.* 1978 for further discussion), especially as as the results can be equally well explained by behavioural differences caused by the thermal properties of the differing morphs.

The intended large scale field experiment at Rogate to test for apostatic selection by song thrushes was abandoned due to methodological problems and limited time. Therefore, the effect of frequency on *Cepaea* morph predation was tested using captive song thrushes feeding on an artificial dimorphic population of *Cepaea hortensis*. The results give some indication that selection was frequency dependent, such that the rare morphs were at a selective advantage. However, song thrushes were not found to be ideal experimental animals and fewer predation trials were completed than anticipated. Therefore valid statistical assessment of the frequency-dependent affect was not possible on the small sample size available. Although, further trials would overcome this problem, the use of captive song thrushes is questionable on ethical grounds, because all the birds showed a loss in body condition over the period of their trials.

The effect of morph frequency on predation was also investigated with a marine predator and polymorphic prey. Predation by shore crabs (*Carcinus maenas*) on an artificial dimorphic population of *Littorina mariae* was tested for visual and apostatic selection. Although the results suffered from small sample sizes at some prey frequency combinations, there was clearly no preference for the conspicuous yellow morphs. This was interpreted as evidence that the crabs were not using visual cues to locate their prey. The lack of visual selection by the crabs did not preclude apostatic selection as this behaviour can be caused by a variety of mechanisms, including the response to chemical or tactile cues when searching for prey. However, there was no indication of apostatic selection by the crabs.

The behavioural mechanism behind apostatic selection was investigated using a computer simulation technique with humans as ´predators´. Although this approach has obvious pitfalls and the generality of these experiments are unknown at present, this technique enabled the testing of recently developed animal searching behaviour hypotheses, relevant to the basis of apostatic selection. Initially, a population of dimorphic ´prey´ were generated on a computer screen, and the human ´predators´ had to remove detected prey from the VDU screen with a light-pen. This experiment revealed several aspects of human searching behaviour. First, apostatic selection occurred when the prey were cryptic but not when conspicuous. In trials with unequal prey frequencies the prey detection rate of individual subjects was not related to their degree of selection for the common prey. These results indicate that the observed apostatic selection was caused by some effect of searching for the cryptic prey and was a perceptual limitation rather than an adaptive strategy. Furthermore, the demonstration that apostatic selection only occurred for cryptic prey agrees with previous studies by Bond (1983) and Cooper (1984) with birds. However, the use of the light-pen introduced a substantial time-lag between detection and elimination of the prey and this prevented accurate assessment of detection times. This may have obscurred any effect of apostatic selection on the detection effciency.

Examination of the effect of density on apostatic selection showed that the overall degree of selection decreased with increasing density, but the individual effects on the frequency-dependent and frequency-independent components could not be established.

The second series of computer simulation experiments were carried out in which cryptic prey images were presented singly amongst a series of blank screens. The subjects only had to detect whether a prey item was present. Thus the light-pen was not used in these experiments. On the basis of predictions by Guilford & Dawkins (1987) the subjects were tested to establish whether they detected the cryptic prey by the development of search images (*sensu* Dawkins 1971a) or whether the subjects modified their search rate (Gendron & Staddon 1983). The results indicated that the detection of common cryptic prey did not interfere with the ability to detect other prey. Also some subjects appeared to modify their search rates on the basis of their detection success. Both these results support the search rate hypothesis of Guilford and Dawkins (1987) and provide no evidence for search image development. However, apostatic selection (for both prey) was also demonstrated in the experiment. This cannot be explained by the search rate hypothesis and suggests that search images were formed for both prey when common. Furthermore, the results of this experiment and previous studies do not support the hypothesis for search image interference, at least in humans. Therefore, the case for search image development as a behavioural phenomena remains unresolved.

Irrespective of the underlying mechanism, the demonstration of apostatic selection in this experiment provides the first evidence that predators may select sequentially encountered single prey in an apostatic manner. All previous apostatic selection experiments have presented populations of prey, such that there is always a choice of prey items within reach of the predator. This experiment is more realistic in representing the distribution of natural prey and their mode of encounter for most predators.

In general, this research study has provided some further information on whether or not predators (a) exert visual selection on polymorphic prey and (b) feed in an apostatic manner that may contribute to the maintenance of the polymorphism, and progress has been made on our understanding of the underlying behavioural mechanism behind apostatic selection. Indeed, as is often the case in research, more questions have been raised than answers. Some promising avenues for future enquiry.

FUTURE RESEARCH

The use of captive predators and live natural polymorphic prey is fraught with problems. However, there is one predator-prey system that appears to be particularly promising. Reimchen (1979) obtained evidence of visual selection on *Littorina* by the blenny (*Blenius pholis*) in experiments carried out in the laboratory. This would probably provide an ideal system for testing apostatic selection as a factor controlling the polymorphism in *Littorina*. Although shore crabs (*Carcinus maenas*) also feed on *Littorina* and are easily maintained in captivity, they have slow predation rates and do not appear to show selective predation on the colour morphs (chapter 4).

The computer based experiments (chapters 5 & 6) were useful for initial testing of the predictions of recently developed theories (e.g. the search rate hypothesis of Guilford & Dawkins (1987)). However the findings of these experiments now need to be tested on real predators. Probably the best candidate for these experiments is the quail (*Coturnix coturnix*) as this has been successfully used for apostatic selection experiments in two previous studies (Cook & Miller 1977; Gendron 1987). With the use of modern high resolution video recording techniques combined with automated computer event recording, many of the variables measured in the human computer experiments could also be accurately assessed for animals.

Clarke (1962a) orginally suggested apostatic selection as a mechanism that may maintain the polymorphism in *Cepaea*. However, to date there is no direct evidence to support this. Surely the time must now be ripe to follow the example of Reid (1987) and test the hypothesis by a large scale field experiment based upon the establishment of artificial *Cepaea* colonies of differing morph frequency. Although the resources needed for such an ambitious experiment are extremely large, the potential importance of the result should not be underestimated.

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Appendix 1. Example Basic program used in experiments reported in Chapter 5; Experiment 1a (cryptic prey).

```
 10CLEAR:CLS
 20MODE 7
 30PRINT
 40 PRINTCHR$(131)"      SIMULATION EXPERIMENT"
 50PRINT'
 60 PRINT"  PROCEDURE"
 70PRINT
 80PRINT"1. An arena will be presented on the"
 90PRINT"screen consisting of a yellow"
100PRINT"background with scattered 'prey' of"
110PRINT"the same colour. These prey items are"
120PRINT"represented by two different shapes"
130PRINT
140PRINT"2. Your task is to locate and delete"
150PRINT"either prey using the light pen as"
160PRINT"FAST AS YOU CAN. The trial will be"
170PRINT"stopped automatically as soon as you"
180PRINT"have deleted half the prey."
190PRINT
200PRINT"3. Prey are deleted from the screen"
210PRINT"by placing the light pen against the"
220PRINT"glass directly over the prey item and"
230PRINT"pressing key Z simultaneuosly."
240PRINT
250PRINTCHR$(129)"Press any key to continue"
260a$=GET$
270CLS
280PRINT
290PRINT"Successful deletion is indicated by a"
300PRINT"short audible 'bleep'. However, you"
310PRINT"may find that you need several "
312PRINT"attempts if your aim is not accurate."
315 PRINT
320PRINT"4. Please do not restrict your "
330PRINT"searching to one area of the screen"
340PRINT"but move over the entire arena. DO NOT"
350PRINT"sweep the light pen across the screen"
360PRINT"whilst pressing key Z continously."
370PRINT
380PRINT"5. The experiment will be repeated 10 "
390PRINT"times consecutively and should last"
400PRINT"nolonger than 10 minutes in total."
410PRINT'''''
420PRINTCHR$(129)"Press any key to continue"
430a$=GET$
440CLS
450PRINT''
460PRINT"You should now be ready to begin."
470PRINT"However if you are unsure of the"
480PRINT"procedure please ask."
490PRINT
500PRINT"Remember please carry out the task as"
510PRINT"quickly as possible."
520PRINT
```

```
530PRINT"The prey items will now be shown to"
540PRINT"you for a fixed length of time then"
550PRINT"THE EXPERIMENT WILL BEGIN"
560PRINT''''''''
570PRINTCHR$(129)"Press any key to view prey and start"
580PRINTCHR$(129)"the experiment."
590a$=GET$
600MODE1
610VDU23,241,0,28,54,99,54,28,0,0
620VDU23,242,0,0,126,126,24,24,24,0
630PRINT''
640PRINT"         THESE ARE THE PREY ITEMS"
650COLOUR 2
660VDU4
670VDU31,15,8
680VDU241
690VDU31,25,8
700VDU242
710VDU30
720Q=TIME+1000
730REPEAT
740UNTIL TIME>=Q
750CLS
760CHAIN"FDSP1"
770END

 10 CLS:CLEAR:VDU20
 20 *TV0,1
 30 *FX11,0
 40 MODE1
 50 ON ERROR GOTO 1310
 60 DIM FRQ(7):MODE1
 70 PRINT
 80 INPUT"EXPERIMENT CODE ? "E
 90 FOR X=1 TO 7
100 READ FRQ(X)
110 NEXT
120 DATA 2, 4, 10, 20, 30, 36, 38
130 NA=FRQ(E):NT=40:NB=NT-NA:R=1
140 DIM SEQ(NT):DIM T(NT)
150 corr%=1542:xcorr%=2:nhd%=80
160
170 VDU23,240,128,30,118,99,182,28,64,17
180
190 VDU23,241,161,18,127,127,28,152,88,17
200
210 VDU23,242,129, 18, 72,  5,160,  4, 64,17
220 DIM CODELOC 50:PROCass
225 IF R=10 THEN GOTO 1310
230 PROCpatt
240 SCOREA=0:SCOREB=0:TIME=0
250 Z=1:COLOUR 2
260 REPEAT:VDU23,1,0;0;0;0;
270 G=GET
280 PROCPENLOC
290 Q=0
300 IF char%=240 PRINTTAB(x%,y%);CHR$(242);
    :SCOREA=SCOREA+1:VDU7:Q=1:GOTO320
```

```
310 IF char%=241 PRINTTAB(x%,y%);CHR$(242);
    :SCOREB=SCOREB+1:VDU7:Q=2 ELSE GOTO340
320 SEQ(Z)=Q:T(Z)=TIME/100
330 Z=Z+1
340 VDU30:UNTIL SCOREA+SCOREB>=(NT)/2
350 PROCtable
360 R=R+1:CLS:VDU20:GOTO 225
370 END
380 DEFPROCPENLOC
390 LOCAL R,C,hreg,lreg,xyval:R=16
400 CALL CODELOC
410 hreg=(?&70 AND 63)
420 lreg=?&71
430 xyval=(hreg*256+lreg)-corr%
440 y%=(xyval DIV nhd%):x%=((xyval MOD nhd%)/xcorr%)+1
450 VDU31,x%,y%
460 PROCchar
470 ENDPROC
480 DEFPROCpatt
490  VDU19,1,0,0,0,0
500 VDU19,2,0,0,0,0
510 VDU5:PLOT4,100,950
520 PRINT"PLEASE WAIT"
530 GCOL0,2
540 FOR X=0 TO 800
550 PLOT4,RND(1200),RND(800):VDU242
560 NEXT
570 VDU4
580 N=0:REPEAT:VDU23,1,0;0;0;0;
590 COLOUR 2:x=RND(37):y=RND(23)+7
600 VDU31,x,y:PROCchar
610 IF char%<>240 N=N+1:VDU31,x,y:VDU240
620 UNTIL N=NA
630 N=0:REPEAT
640 x=RND(37):y=RND(23)+7
650VDU31,x,y:PROCchar
660IF char%<>241 AND char%<>240 N=N+1:VDU31,x,y:VDU241
670 UNTIL N=NB
680 VDU30
690 VDU5:GCOL0,3
700 PLOT4,100,900
710 PRINT"READY - PRESS ANY KEY TO START TRIAL."
720 a$=GET$
730 VDU20:VDU4:VDU19,3,0,0,0,0
740 ENDPROC
750
760 DEFPROCass
770 FOR PASS=0 TO 2 STEP 2
780 P%=CODELOC
790 [OPT PASS
800 LDA#16
810 STA &FE00
820 LDA &FE01
830 STA &70
840 LDA#17
850 STA &FE00
860 LDA &FE01
870 STA &71
```

```
 880 RTS
 890 ]
 900 NEXT PASS
 910 ENDPROC
 920
 930 DEFPROCchar:A%=&87:X%=0:Y%=0
 940 C=USR(&FFF4)
 950 char%=(C AND &FFFF)DIV &100
 960 IF char%>=128 THEN char%=char%+96
 970 ENDPROC
 980 DEFPROCtable
 990 CLS:PRINT
1000 PRINT" TRIAL COMPLETE - PLEASE WAIT"
1010 COLOUR 3
1020 VDU2:PRINT
1030 PRINT"TRIAL ";R
1040 PRINT
1050 PRINT"PREY 1 = ";NA;"  PREY 2 = ";NB
1060 PRINT
1070 PRINT TAB(10);"PREY";TAB(15);"TIME";TAB(25);"INTERVAL"
1080 PRINT:FOR X=1 TO NT/2
1090 PRINT TAB(5);X;TAB(10);SEQ(X);:@%=&02020A:
     PRINTTAB(15);T(X);TAB(25);T(X)-T(X-1)
1100 @%=&090A
1110 VDU23,1,0;0;0;0;
1120 NEXT
1130 EA=NA-SCOREA:EB=NB-SCOREB
1140 IF EA=0 THEN NA=NA+1:EA=EA+1
1150 IF EB=0 THEN NB=NB+1:EB=EB+1
1160 @%=&090A
1170 A=LOG(NA/EA)
1180 A=A/((LOG(NB/EB))+(LOG(NA/EA)))
1190 B=DEG(ASN(SQR(A)/100))
1200 G=ASN(SQR(A))
1210 B=DEG(G)
1220 PRINT
1230 PRINT "PREY 1 SCORE = ";SCOREA
1240 PRINT
1250 PRINT "PREY 2 SCORE = ";SCOREB
1260 PRINT
1270 VDU3
1280 VDU23,1,1;0;0;0;
1290 ENDPROC
1300
1310 VDU23,1,1;0;0;0;
1320 *FX12,0
1330 VDU4
1340 VDU20
1350 MODE1
1360 END
```

Appendix 2. Example Basic program used in experiments reported in Chapter 6; Experiment 2, Prey 1 frequency = 0.167.

```
 10CLEAR:CLS
 20MODE 7
 30PRINT
 40 PRINTCHR$(131)"      SEARCH EXPERIMENT"
 50 PRINT
 60 PRINT"          PROCEDURE"
 70PRINT
 80PRINT"1. An arena will be presented on the"
 90PRINT"screen consisting of an orange"
100PRINT"background with OR without a ´prey´"
110PRINT"item of the same colour."
120PRINT
130PRINT"2. Your task is to search for the prey"
140PRINT"item. If you find it you must"
150PRINT"IMMEDIATLEY press EITHER key ´1´ if it"
160PRINT"is a CIRCLE or if it is a ´T´ press"
161 PRINT"key 2."
163 PRINT
164PRINT"Alternatively as soon as you decide"
170PRINT"that no prey is present you must press"
180PRINT"key ´0´."
190 PRINT
200PRINT"3.You must carry out this task AS FAST"
210PRINT"AS POSSIBLE."
220 PRINT
230PRINT"Press any key to continue"
240a$=GET$
250CLS
251 PRINT
252PRINT"4. An audible ´bleep´ will be emmitted"
253PRINT"if you wrongly press key 1 OR 2, when"
254PRINT"no prey item is present."
260PRINT
270PRINT"5. The experiment will be repeated 45 "
280PRINT"times consecutively and should last"
290PRINT"no longer than 15 minutes in total."
300PRINT´
310PRINT"You should now be ready to begin."
320PRINT"However if you are unsure of the"
330PRINT"procedure please ask."
340PRINT
350PRINT"Remember please carry out the task as"
360PRINT"quickly as possible."
370PRINT
380PRINT"The prey item will now be shown to"
390PRINT"you for a fixed length of time then"
400PRINT"THE EXPERIMENT WILL BEGIN"
410 PRINT´
420PRINT"Press any key to view prey and start"
430PRINT"the experiment."
440a$=GET$
450MODE1
460VDU23,241,0,28,54,99,54,28,0,0
462VDU23,242,0,0,126,126,24,24,24,0
```

```
470PRINT''
480PRINT"         THESE ARE THE PREY ITEMS"
490COLOUR 2
500VDU4
510VDU31,12,8
520VDU241
523VDU31,10,12:PRINT"PREY 1"
525VDU31,25,8
526VDU242
527VDU31,22,12:PRINT"PREY 2"
530VDU30
540Q=TIME+1000
550REPEAT
560UNTIL TIME>=Q
570CLS
580CHAIN"FSQ1"
590END
```

```
 10 CLS:CLEAR:VDU20
 20 *TV0,1
 30 *FX11,0
 40 MODE1
 50 T0=0:T1=0:T2=0
 60 C0=0:C1=0:C2=0
 70 VDU23,240,128,30,118,99,182,28,64,17
 80 VDU23,241,161,18,127,127,28,152,88,17
 90 VDU23,242,129, 18, 72,  5,160,  4, 64,17
100 DIM RN(45):DIM P(45)
110 DIM SEQ(45):DIM ATIME(45):DIM ANS(45)
120 PRINT''
130 PRINT"               PLEASE WAIT"
140 X=1
150 P=RND(45):C=0
160 FOR A=1 TO X
170 IF P=RN(A) THEN C=1
180 NEXT
190 IF C=1 GOTO 150
200 IF X=45 GOTO 220
210 RN(X)=P:X=X+1:GOTO 150
220 RN(X)=P
230 FOR A=1 TO 45
240 READ SEQ(A)
250 NEXT
260 DATA 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,1,1,1,2,2,2,2,2,2,
    2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2
270 FOR Y=1 TO 45
280 R=RN(Y)
290 P(Y)=SEQ(R)
300 CLS:VDU20
310 PROCpatt
320 *FX15,0
330 COLOUR 3:VDU30:VDU 23,1,0;0;0;0;
340 PRINT''''
350 PRINT"    PRESS ANY KEY TO START TRIAL"
360 B=GET
370 VDU19,2,3,0,0,0:VDU19,3,0,0,0,0
380 TIME =0
```

```
390 K=GET:T=TIME/100
400 IF NOT (K=49 OR K=48 OR K=50) GOTO 390
410 IF K=49 THEN ANS(Y)=1
420 IF K=49 AND P(Y)=0 THEN VDU7
430 IF K=48 THEN ANS(Y)=0
440 IF K=50 THEN ANS(Y)=2
450 IF K=50 AND P(Y)=0 THEN VDU7
460 ATIME(Y)=T
470 IF P(Y)=0 AND K=48 T0=T0+T:C0=C0+1
480 IF P(Y)=1 AND K=49 T1=T1+T:C1=C1+1
490 IF P(Y)=2 AND K=50 T2=T2+T:C2=C2+1
500 NEXT Y
510 CLS:VDU20
515 VDU2
520 PRINT TAB(0);"ITEM";TAB(10);"PREY";TAB(20);"ANSWER";
    TAB(35);"TIME"
530 FOR Y=1 TO 45
540 PRINT TAB(0);Y;TAB(10);P(Y);TAB(20);ANS(Y);TAB(30);ATIME(Y)
550 NEXT Y
560 PRINT''
570 PRINT"TOTAL PREY 1 CORRECT = ";C1
580 PRINT"TOTAL PREY 2 CORRECT = ";C2
590 PRINT"TOTAL ABSENCE CORRECT = ";C0
595 IF C1=0 GOTO 605
600 PRINT"MEAN PREY 1 TIME = ";T1/C1
605 IF C2=0 GOTO 615
610 PRINT"MEAN PREY 2 TIME = ";T2/C2
615 IF C0=0 GOTO 630
620 PRINT"MEAN GIVE UP TIME = ";T0/C0
630 VDU3
640 *FX12,0
650 VDU 23,1,1;0;0;0;
660 END
670 DEFPROCpatt
680 VDU19,2,0,0,0,0:VDU5:PLOT4,100,950
690 PRINT"            STANDBY"
700 GCOL0,2
710 FOR X=0 TO 800:PLOT4,RND(1200),RND(800):VDU242:NEXT
720 VDU4:COLOUR 2:IF P(Y)=0 GOTO 750
730 x=RND(37):y=RND(23)+7:VDU31,x,y,
740 IF P(Y)=1 VDU240 ELSE VDU241
750 VDU19,1,0,0,0,0
760 ENDPROC
```

Appendix 3.

A published paper

The following published papers were included in the bound thesis. These have not been digitised due to copyright restrictions, but the links are provided.

https://doi.org/10.1038/hdy.1988.50