

UNIVERSITY OF SOUTHAMPTON

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES

School of Biological Sciences

**Selection by Wild Birds Foraging on Artificial Prey in
Heterogeneous Backgrounds**

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ABSTRACT
FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES
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HETEROGENEOUS BACKGROUNDS

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Many animals that are prey to animals that hunt by sight tend to rest in places that are similar to them in colour, texture, and other visual properties and they thus minimise the probability of being detected. Such an animal is said to be 'cryptic'. Within prey species living in heterogeneous backgrounds this could result in the evolution of several different colour morphs with the fitness of each morph being related to its degree of crypsis in the background. At equilibrium the frequencies of the morphs will be proportional to the frequencies of their matching background elements and this relationship could contribute to the maintenance of the polymorphism. The experiments in much of the thesis attempted to determine (1) whether birds are more likely to eat prey in unmatching backgrounds that make them conspicuous rather than prey in matching backgrounds that make them inconspicuous and (2) whether birds select in a more strongly apostatic fashion when presented with different proportions of two colours of prey in backgrounds that make them inconspicuous in comparison to when the same prey are presented in backgrounds that make them conspicuous. In the last section of the thesis I try to determine whether proximity of a prey to stones has an effect on its risk of predation and, if so, why.

I present the results of five sets of experiments with wild birds and artificial prey. In two experiments (Chapter III) two prey types were presented to predators in equal frequencies (to test for frequency independent selection). Three experiments (Chapter IV) used different prey frequencies (testing for frequency dependent selection). In all cases the experiment trials were stopped when half of the prey had been eaten and selection then was measured. Different components of these experiments were carried out in Culiacan, Mexico and Southampton, England. In backgrounds of coloured stones that made one of the prey inconspicuous, birds tended to concentrate on the conspicuous (unmatching) prey. This selection against the unmatching form was stronger when the prey were presented in high density backgrounds (600 stones) than in low density backgrounds (200 stones). In backgrounds where both prey were equally cryptic but presented in different frequencies the predators tended to concentrate on the most common type and overlooked the rare ones. This 'apostatic selection' was more accentuated when the stones were denser, perhaps because the prey were more difficult to detect and the birds therefore concentrated their efforts on the colour they encountered more frequently.

When prey were presented in equal frequencies selection was dependent on the background composition. These results lend support to the idea of parallelism given by Endler in 1978, because this kind of selection should result in a neutral equilibrium, with morph frequency depending of the background composition. In the experiments described in Chapter IV apostatic selection was stronger when prey was in backgrounds that made them inconspicuous (the backgrounds used were natural grass and soil and stones that matched the prey colours on hessian sheets). This implies the adoption of search images.

In Chapter V, three experiments (in Southampton, England) tested the effect of distance to the stones on the risk of predation and showed that stones offered more protection to the prey that matched the closest stone. Resting close to the stones offered protection from predation regardless of the colour of the stone.

In summary the results of my work from both Mexico and the UK, strongly support the general idea that apostatic selection is most effective when prey match the colour of the background.

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Chapter I

Introduction

Introduction

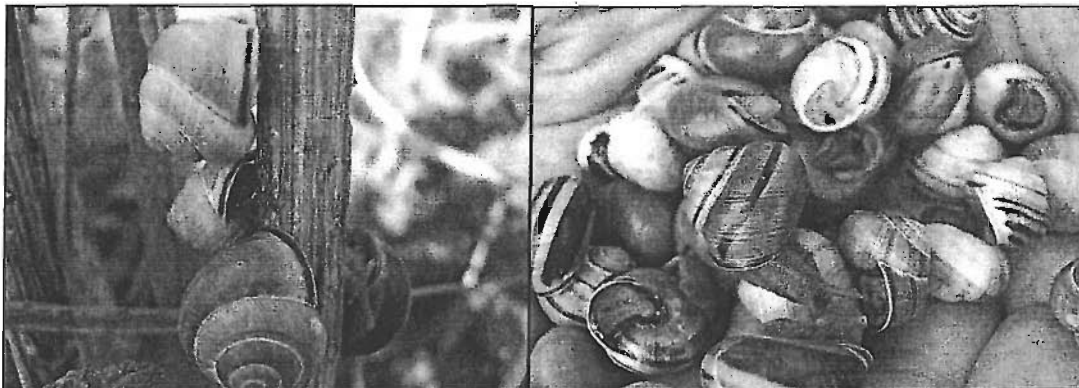
It is a well-known fact that many palatable animals tend to rest in places that are similar to them in colour, texture, and other properties and thus avoid being detected by predators that hunt by sight. Such an animal is said to be 'cryptic' (Cott, 1940; Edmunds, 1974). The best-protected prey will be the one that has the most resemblance to the background on which it rests (Endler, 1978) and thus natural selection by predators favours those individuals that are most cryptic (Poulton, 1890; Edmunds, 1974; Cott, 1942).

In this investigation I aim to explore the relationship between crypsis and colour polymorphism. Such polymorphism is defined as the occurrence in a population of several genetically correlated phenotypic forms at frequencies too high to be explained by mutation alone. The first one to recognise the adaptive significance of polymorphism in cryptic prey was Poulton (1884) when he argued that a cryptic polymorphic prey population is capable of living in a wider range of backgrounds than a monomorphic population. Two examples of polymorphic species are shown in Figures 1.1 and 1.2.

Endler (1978) suggested that the frequencies of cryptic morphs at equilibrium would be proportional to their levels of crypsis in the population. For example, when there are two cryptic morphs and one is similar to the colour pattern of the least common colour element in the background, while the other one is most similar to the most common colour pattern, then the second one will have a higher level of crypsis and thus will be better protected. Therefore selective predation will result in the frequencies of the morphs becoming proportional to the frequencies of the elements of the background to which they are similar. This is important because it is believed that this relationship could contribute to the maintenance of polymorphism in cryptic polymorphic prey (Endler, 1978; Bond and Kamil, 1998). Another important factor that could contribute to the maintenance of polymorphism is apostatic selection, which implies that selection by predators against a prey type increases as the frequency of that prey increases or in other words, predation on the most abundant forms in a population, leading to a balanced distribution of a variety of forms. (Clarke, 1962; Allen, 1989). This flexibility in the selection of the prey with respect to availability can promote polymorphism in populations and even, perhaps, communities of species (Figures 1.1 and 1.2) (Clarke 1962, Ayala and Campbell 1974). The work in this thesis is about the interaction between crypsis and apostatic selection.

(1.1) Frequency-Dependent Selection in Non-Matching Backgrounds

The first to demonstrate that wild birds, important predators of polymorphic species, could exert apostatic selection were Allen and Clarke (1968). They use dimorphic prey made with flour and lard in two colours, brown and green. Their experiments had two main conclusions. First, birds selected the colours of prey to which they had previously been conditioned; that is the colour that was effectively commonest. Second, untrained birds, when presented with baits populations in which one type of bait was 9 times more common than the other, tended to select the commoner colour. Further work with birds and baits has confirmed the plausibility of apostatic selection (Allen, 1972, 1973, 1974; Manly *et al*, 1972; Cook and Miller, 1977, Church *et al*, 1997). In all these experiments the prey were conspicuous.



Figures 1. 1 and 1. 2. Polymorphism in *Cepaea nemoralis* and *Cepaea hortensis* (Photographs by K. Cruickshanks).

As an extension of Allen and Clarke (1968), Allen (1976) in 14 experiments presented populations of green and brown baits to untrained wild birds in their normal surroundings. In seven of the 14 experiments birds were presented with 9 green: 1 brown populations for a number of days, followed by 9 brown: 1 green population for a similar period. In the rest of the 14 experiments (the remaining 7) the birds were presented with the same populations but in a reverse order. The results were very variable, but in every experiment there was good evidence that birds tended to concentrate on the common colour.

Weale *et al* (2000) compared four different experiments, conducted at different times and with different designs, for exploring the relationship between frequency-dependent selection and prey density in wild birds feeding on pastry prey. One experiment used pastry baits that differ only in the presence or absence of a red stripe and in this case they did not find any selective behaviour. But in the other three experiments (using green and brown baits) they found evidence that anti-apostatic selection increases when the density increases (>100 baits m^{-2}). One of these experiments

(experiment 3) provided no evidence of frequency-dependent selection at low densities (0.5-20 baits m⁻²). The other two experiments showed evidence that apostatic selection (selection against the common form) increases when prey are at low densities (down to 2 baits m⁻²). Appears that frequency-dependent selection can be modified by density, in other words, it seems that there is a threshold where predators change their attention to the common form, maybe because when prey are at high densities the rare form is more visible in the 'sea' of common forms.

In three natural populations of male guppies (*Poecilia reticulata*) the frequencies of different conspicuous colours patterns were manipulated, to estimate survival rates. Rare phenotypes were found to have had a highly significant survival advantage compared to common phenotypes. This study provides support for frequency-dependent survival, presumably linked to predation (Olendorf *et al*, 2006).

But do predator select apostatically when the prey are inconspicuous or cryptic, in other words, under circumstances when selection is usually expected to be frequency independent?

(1.2) Frequency-Dependent Selection in Matching Backgrounds

Many cryptic animals are also polymorphic, occurring in multiple and distinctive patterns within the same populations. Prey diversity in such species may be maintained and promoted through apostatic selection (Bond and Kamil, 2002). This cryptic polymorphism has been recorded in different taxa, such as grasshoppers (Dearn 1990), Homoptera (Halkka and Halkka 1990), mantids (Edmunds 1990), and bivalves (Whitley, Owen and Smith 1997).

In 1941 and 1942 Popham used different forms of the camouflaged corixid bugs (*Arctocoria distincta*) as prey at different frequencies. When the predator (Rudd, *Leuciscus erythrophthalmus*) faced three forms instead of two, even the most cryptic form became disadvantageous when it occurred at relatively high frequencies. Experiments with humans also suggest apostatic selection when subjects are asked to search on a computer screen for different virtual prey types in complicated matching backgrounds (Tucker and Allen 1988).

Cooper (1984a and b) found evidence that apostatic selection is stronger when prey rest in heterogeneous backgrounds where they resemble elements of the background. His experiments used two types of pastry baits (orange and grey). He made the baits inconspicuous by scattering them over a hessian sheet partially covered with different frequencies of stones of two colours (orange and grey). The strength of apostatic selection was stronger in this type of background

compared with backgrounds of hessian and stones that made the prey conspicuous. I found some evidence supporting this point when in Mexico I performed a set of experiments using two colours of dog pellets (green and brown) with different frequencies in natural environments as backgrounds (grass and soil). The results tended to suggest that apostatic selection is stronger when the pellets were inconspicuous (Sánchez-Zazueta, unpublished).

The first controlled experiment to test the effect of visual predators on prey that are both cryptic and polymorphic used blue jays (*Cyanocitta cristata*) searching for 'digital moths' on a computer monitor. Moths evolved via a genetic algorithm in which individuals detected by the jays were less likely to 'reproduce'. Jays often failed to detect atypical cryptic forms, confirming frequency-dependent selection and suggesting the use of search images, which enhance the detection of common prey (Timbergen, 1960; Dawkins, 1971). Over successive generations, the moths evolved to become significantly harder to detect, and they showed significantly greater phenotypic variance than the frequency independent controls (Bond and Kamil, 2002).

Littoraria filosa (Sowerby) is a marine snail of the *L. scabra* group, that lives amongst the foliage of mangrove trees in northern Australia and was studied by Reid (1987). The colour of the shell is polymorphic, showing two discrete ground colours, yellow or orange, with some brown patterning. In a site on Magnetic Island, northern Queensland, colour frequencies of small snails were similar on different backgrounds. Amongst larger shells, yellows were more frequent on *Avicennia* trees with abundant foliage, and orange on relatively bare trees, suggesting that visual selection for crypsis occurred. There was no evidence of substrate selection by the morphs. Temperature measurement showed that yellow shells were cooler than orange shells, but differences in colour frequencies on sunny and shaded trees, and at different seasons, did not suggest climatic selection. By manipulating the colour frequencies of subpopulations of small snails isolated on individual trees, Reid showed that the disappearance of yellow and orange shells was frequency-dependent. This result lends support to the hypothesis of matching of background elements by the morphs and of apostatic selection by unknown predators. Only the latter can account for the persistence of the highly conspicuous pink morph at low frequencies (Reid, 1987).

(1.3) What is meant by “background matching”?

a) Crypsis & Masquerade

The coloration of animals and their backgrounds are perceived as mosaics that vary in size, colour, reflection of light and form (Endler, 1988). But to be really cryptic, the pattern of coloration must look like a random sample of the coloration patterns of the background as perceived by the predators in the seasons, visual conditions and microhabitats where the prey are most vulnerable to predation (Endler, 1978). The degree of crypsis can be measured by the similarity between the animal and the background with respect to size, colour, reflection of light and the alignment of its body in comparison with the patterns in the background. Conspicuousness is proportional to the divergence in one or more of these characteristics. Numerous experiments and field correlations show that the general tendency of colours and tones of animals is to match the background where they live (Cain and Sheppard, 1950; Kettlewell, 1955; Endler, 1978, 1984, 1991; Whiteley, *et al.*, 1997; Merilaita *et al.*, 1999; Heiling *et al.*, 2003, 2005). Thus crypsis is part of the interaction between an animal and its environment or background and not a property of the species in isolation. In theory, the number of ways to be cryptic will be limited by the heterogeneity and complexity of the background where the animal lives. The majority of natural environments exhibit some level of heterogeneity in their composition either spatially or temporally (Godfrey *et al.*, 1987; Endler, 1990; 1991; Seehausen *et al.*, 1999; Stuart-Fox, *et al.*, 2004). Cryptic and conspicuous coloration (often associated with unpalatability) are the extremes of the spectrum of the patterns of coloration in prey (Endler, 1978, 1984, 1986). But, in practice, most prey species are probably cryptic (only with the exception when crypsis conflicts with the pressures of sexual selection) (Poulton, 1890; Thayer, 1909; Cott, 1940; Edmunds, 1974; Endler, 1978). A list of selected examples that can illustrate the usefulness of being cryptic is given in Table 1.1.

Table 1. 1 Examples of crypsis and masquerade.

Prey species	Background	Reference
<i>Abbotana clemitaria</i> (Butterfly)	Dead leaves.	Holland (1908).
<i>Sabulodes transversata</i> (Butterfly)	Matching the geometry of a dead leaf.	Holland (1908).
<i>Philaeneus spumaris</i> (Spittle bug)	Cryptic with vegetation	Halkka (1962)
<i>Arcottetlix rabula</i> (Grasshopper)	Cryptic on desert rocks and plants	Gillis (1982)
<i>Bupalus piniarius</i> (Pine looper)	Good match for pine needles	Den Boer (1971)
<i>Littorina obtusata</i> (periwinkle)	Seaweeds or part of seaweeds	Smith (1976)
<i>Lihorina mariae</i> (periwinkle)	Seaweeds and rocks	Reimchen (1979)
<i>Cepaea nemoralis</i> (Snail)	Woodland, grassland, sand dunes, etc. in Britain.	Richardson (1975).
<i>Arianta arbustorum</i> (Hedge snail)	Brown snails more common in woodland.	Parkin (1971)
<i>Limicolaria martensiana</i> (African snail)	Streaked from appears cryptic.	Owen (1963, 1965)
<i>Sphaeroma rugicauda</i> (Marine isopod)	Mud and in vegetation	West (1964)
<i>Equus burchellii</i> (Zebra)	Open Savannah	Pietrewicz and Kamil (1977).
<i>Pyrrhocorax graculus</i> (Bird – Crow)	Rocks, snow, etc.	Rothschild (1975).
<i>Phrynobatrachus</i> sp. (Frogs)	Colour patterns appear cryptic	Stewart (1974)
<i>Chamaleo</i> and <i>Anolis</i> (Lizards)	Tree trunks, leafs, bark, etc.	Endler (1986).
<i>Mantis religiosa</i> (Mantid)	Grass, leaves, etc.	Cesnola (1904).
<i>Ptychozoon kulhi</i> (Gecko – lizard)	Tree trunks.	Tweedie (1960).

If the background is formed of many patches of different colours, then there are many possible combinations of colours that can make an animal cryptic. Thus the more heterogeneous and complicated the background the greater the number of possible cryptic forms. The variety of background components is therefore expected to be a factor in promoting a variety of patterns of coloration in a polymorphic population (Copper, 1984b; Cook, 1986, 1998; Allen, 1988; Deutsch, 1997; Merilaita, 2001).

Predators searching for prey need to detect objects that are different in some way from the coloration of the background. The probability of such an object being detected is inversely proportional to its level of the crypsis. If the similarity of an organism to a particular element of the background is too perfect, this reduces the places in which it can be cryptic and this can affect their ecology in general. Endler (1986) called such a situation 'masquerade' rather than crypsis. Thus an insect masquerading as a thorn of a particular species of shrub is limited to the places where it is afforded protection. Geometrid caterpillars, stick insects (genus *Timema* (Sandoval, 1994)) and praying mantids (e. g. *Hoplocorypha*, *Danuria* and *Stenovates*) are a good examples of masquerading animals (Edmunds 1974). The main difference between crypsis and masquerade is that when an animal is cryptic the predator fails to pick up any signals from the prey animal, but in the case of masquerade the predator detects the prey but fail to recognize them as being edible (Robinson 1969).

Edmunds (1974) explains in detail the limitations of crypsis. First, to remain undetected a cryptic prey must not move, because movement alert a predator near by. Therefore locomotion must either be very slow, for example so that it resembles the movements of plants by the wind, or the animal must remain motionless until the danger has passed. Second, when remaining motionless for long periods the animal cannot feed, drink or mate. Thus many cryptic animals are more active during night than during day. Third, animals must find an appropriate place to rest to be inconspicuous. For example, a green grasshopper is well concealed in green vegetation, but it becomes conspicuous when it rests on soil or sand. Selection will tend to eliminate any individual resting in the wrong place, and may favour genes that cause the animal to choose a matching background. For example, Sargent (1968) found that a dark moth (*Catocala antinympha*) rest more often on dark surfaces than a pale moth (*Campaea perlata*) that prefers to rest on white surfaces and this difference in choice of background is genetically determined (Sargent, 1969a). Fourth, predators that hunt by search image (see next section) could learn to distinguish the patterns of the cryptic prey and the advantage of crypsis will diminish. The principal ways in which predators overcome crypsis are through either accidentally or through systematic search finding a prey animal, develop a searching image for that particular type and then search for more individuals in the environment. This is unlikely to happen if the prey species is rarely encountered, as the predator will soon forget

the search image. Cryptic species will be more protected if they rest spaced out, so that predators cannot form search images easily (Tinbergen et al., 1967). That predator selection is responsible for this spacing out is suggested by the fact that the fish *Vimba vimba* deposits spawn in compact masses if there are no predators, but scatters it when predators are present (Tinbergen et al., 1967; Croze, 1970).

If hunting by searching image is common it is likely that predator selection will normally set a limit to the density of a cryptic prey species. If the prey is too common, hunting by searching image will occur and predation will be very intense so that the proportion of prey surviving will be low. If prey is less common then predators will not hunt by searching image; predation will be weaker and the proportion of prey surviving will be higher. A possible way in which a scattered cryptic species can become more common without being at more risk of predation is by occurring in several different colour morphs (Tinbergen et al., 1967).

When one morph in a polymorphic population is much commoner than another morph it is likely that predators may build up a search image for the commoner morph but not for the more rare form (Edmund, 1974). Therefore more of the common form should be preyed on relative to its frequency in the population. This is 'apostatic selection' (Clarke, 1962) or 'reflexive selection' (Moment, 1962), and it is a form of frequency-dependent selection (Murray, 1972).

(1.4) How do predators detect cryptic prey?

The behavioural mechanism that enables predators to detect cryptic prey is still a subject of debate. The two main hypotheses have been assigned the following names: 'Search image' and 'Search rate'.

A search image is the perceptual improvement in the ability to detect a cryptic prey (Tinbergen 1960, Dawkins 1971). It is believed that this is due to the ability of individuals to learn those cues that distinguish prey from the background (Bond 1983, Lawrence and Allen 1983, Gendron 1986), such as shape or a slight difference in colour. Thus the success of a predator in finding camouflaged prey depends much on its ability to make distinctions in its visual world. Maximizing the efficiency in the making of decisions depends on advanced perceptual and visual processing systems. These two qualities are very related, so that the first would not serve without the other one (Croze, 1970). It is thought that if the 'search image' to a morph is formed faster and retained for more time due to the high number of encounters (evidence is scarce) (Tinbergen 1960, Dawkins 1971), then that prey is at more risk when its frequency increases (Allen 1988, Clarke 1962, Greenwood 1984) and hence the maintenance of polymorphism through apostatic selection.

On the other hand the hypothesis of 'search rate' assumes that it is possible for predators simply to slow down their rate of search to allow the visual system to detect the prey. They thus adjust their 'search rate' to the level of crypsis of the prey (Guilford and Dawkins 1987). Gendron (1982) observed such a decrease in search speed among bobwhite quail, *Colinus virginianus*, when their prey becomes more cryptic. Similarly, Goss-Custard (1977) found that the speed of redshanks searching for worms decreased as the mean size and presumably the conspicuousness of the worms decreased. Smith (1974) found that blackbirds, which utilize a stop and go search tactic, spent more time scanning at each stopping point when the prey more closely resembled the background.

To the predator, the disadvantage of developing a 'search image' is that it will cause interference, because once the 'search image' is developed for a type of prey, the predator will lose the capacity to detect other prey types with the same level of crypsis. However the hypothesis of 'search rate' does not have that type of restriction, because predators using this strategy would detect all types of equally cryptic prey that they encounter. If sight-dependent predators always slow down their search rate to detect cryptic prey then clearly polymorphism could not be maintained. Thus the 'search image' versus 'search rate' controversy is central to the study of the maintenance of colour polymorphism but is outside the brief of my work.

(1.5) Aims

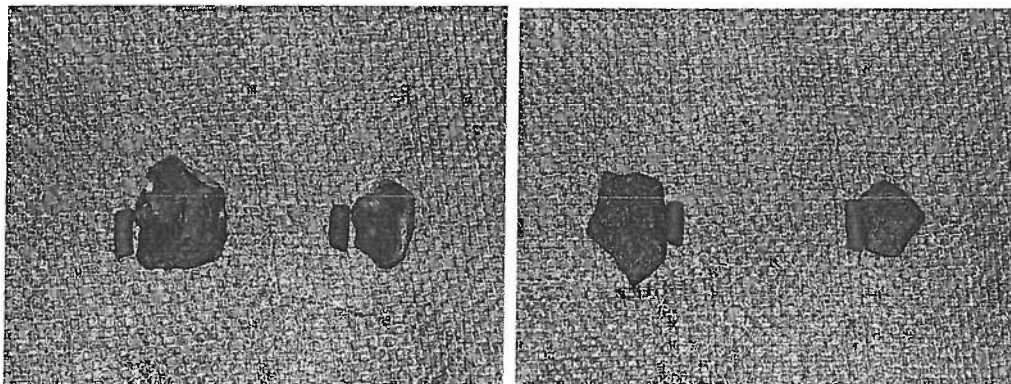
In this thesis I present the results of experiments mostly using artificial prey in backgrounds of stones (after Cooper 1984b) designed to test the relationship between frequency dependent selection and crypsis.

The aims of the work were:

1. To test whether ground-feeding birds are more likely to eat prey in unmatching backgrounds that make them conspicuous rather than prey in matching backgrounds that make them inconspicuous.
2. To test whether birds select in a more strongly apostatic fashion when presented with different proportions of two colours of prey in backgrounds that make them inconspicuous in comparison to when the same prey are presented in backgrounds that make them conspicuous.
3. To test whether apostatic selection becomes stronger when the complexity (number of stones) of the background is increased.
4. To investigate whether proximity of a prey to stones has an effect on its risk of predation and, if so, why.
5. To establish whether any trends observed are applicable to selection by wild birds in both the UK and Mexico

Chapter II

Materials and Methods



Introduction

The use of pastry baits (usually made from lard and flour in a 1:3 or 5:12 ratio) in this type of experiment is the easiest and most practical, because they can be readily manipulated with respect to such factors as colour, shape and size. This also avoids the use of natural prey, which could be unethical, not to mention the large amount of time that it would take to collect live specimens. Pastry baits have been widely used before without serious criticism (Allen 1972, 1973. Cooper 1984a and b). Besides, this technique has stood the test of time; and there are no reports that the baits have any ill effect in birds. Actually the pastry baits are probably highly nutritious to the birds, because these contain fat, carbohydrate and various vitamins, particularly important in cold weather.

The materials and methods described below are what I used 'generally' during the experiments in this report. Materials and methods that were specific for each experiment are given in the appropriate chapter.

(2.1) Prey

a) Manufacture

In most of the experiments the baits were made from a mixture of plain flour and lard in a ratio of 12:5 by weight (Cooper, 1984). The flour and lard was mixed using a Kenwood Chef food mixer. I then used a modified mincer attachment in the same mixer to produce 'worms' which I then cut in to small cylinders 6.5 mm in diameter and 10 mm long in two colours, brown and grey (Cooper, 1984). My 'brown' is the same as Cooper's 'orange'. For the grey baits I used 7.5 ml of food dyed black (K 6028) and for the brown baits I used 2 ml of orange (K6015) and 7.5 ml of caramel (K6025) (Cooper, 1984) (Table 2.1). Pointing Ltd., Northumberland, England, manufactured the food dyes. The baits produced were stored in sandwich boxes inside a fridge at about 5°C, where they could be kept without obvious signs of deterioration for several months.

Table 2.1 Colours of pastry baits. Manufacturers name for the food dye, manufacturer code number for each dye. Colours based on the Munsell Color System (1966). Food dyes were manufactured by Pointing Ltd., Northumberland, England.

Baits	Manufacturer name of food dye	Manufacturer code number	Litres per kg of pastry	Hue*	Value chroma*
Undyed	-	-	-	2.5Y	9/2
Brown	Orange +	K 6015	.002	5YR	4/6
	Caramel	K 6025	.0075		
Grey	Black	K 6028	.0075	Gray	4.5/0

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

(2.2) Background

In the first experiment of Chapter 4 (the ‘dog pellets’ experiment) in Culiacán, Mexico, grass and soil was used as background. This was an obvious choice because these resembles the natural habitats of some terrestrial prey like some worms, crickets, etc.

For the rest of the experiments I used variations of Cooper’s (1984) background design because it was clear that there were plenty of experimental options to be explored with this design. Besides this, the background was practical to use, and the frequencies of elements were fairly easy to change. The background consisted of natural stones of two colours: brown and grey (my ‘brown’ is Cooper’s ‘orange’) resting on a brown hessian sheet, dimensions 1.4 x 4.0 m. The stones were of the type used in road construction, sorted by eye into grey and brown flint. The mean size of the grey stones was 3.75 cm (+/- 0.6 cm) long and 2.75 (+/- 0.7 cm) wide and the mean size for the brown stones was 4.85 (+/- 0.9) long and 3.5 cm (+/- 0.4 cm) wide.

For some of my control experiments (in Chapter III and Chapter IV) I used ‘Oriental Red’ or ‘Ming Claret’ (10-15 cm) and ‘Oriental White’ or ‘Ming Snow White’ (10-15 cm) stones, these are the commercial names commonly used by garden designers in the UK. These stones came from quarried marble boulders that were then crushed into decorative gravel.

(2.3) Predators

The intended predators were wild passerine birds. These are widespread predators with colour vision and are well known to feed on polymorphic prey (Clarke 1962, Reiskind 1965, Goodale and Snedden 1977, Allen 1988). Lists of birds are given for each of the experiments. It is worth mentioning that in most of the experiments in Culiacán, México, 95 % of predators were the long tail grackle *Quiscalus mexicanus*. The predators visiting the experiments in the UK were more variable, but the most common visitors were Blackbirds (*Turdus merula*) and Magpies (*Pica pica*).

(2.4) Procedures

a) Background distribution and randomisation

It is important to randomise the experiment design, because the birds could be capable of identifying a trend and thus predict events, which could then bias the results. The order of sites and order of treatments were also randomised (using a random numbers generator).

As far as possible, I randomised the distribution of stones and prey in all the experiments, except in the experiments described in Chapter V in which prey were deliberately placed at different distances from stones. Any other special distribution or randomisation is explained in the methods for each experiment.

The distribution of the baits over the hessian sheet was made haphazard (or evenly disperse) by dropping handfuls (without looking) from shoulder height. This operation was repeated for any prey that bounced out of the sheet or came to rest on top of a stone.

b) Pre -Training

For the birds to learn to associate a novel background with food, some sort of training is often needed. For this I used undyed baits of the same type as the ones used in the experiments, except they were made without the addition of dye. For about ten days before the experiments, every morning I dropped 50 white baits over the hessian sheet (with no stones on it) and repeated this with new ones every time the baits ran out.

c) Data collection

A trial was deemed to be complete once approximately 50 % of the baits had been removed (Cooper, 1984b). In England there was much variation in the time to complete each trial, even within sites. This depended on the season, the weather and most importantly the bird species feeding on the experiment sites. For example in places where ‘larger’ species like pigeons, magpies or crows were feeding the times were shorter (around 1 hour), but when ‘smaller’ species like robins, sparrows, etc., were the main predators the rate of predation was much slower (sometimes several hours). In Mexico the feeding was more stable and fast; sometimes a trial would last as little as five minutes.

For each trial the numbers of each bait colour taken were recorded. Sometimes the birds were observed while feeding and the sequences of prey captured were also recorded. For some of the experiments photographs of the stones and prey ‘before’ and ‘after’ were taken to test the protection offered by stones (close enough to be able to see the baits). In all trials the numbers and species of birds were recorded and the duration of the trial and the weather conditions were noted.

d) Analysis of the data

The analysis of selective predation experiments method has been the subject of much discussion (Cook, 1965; Elton and Greenwood, 1970; Manly, 1973, 1974; Manley *et al*, 1972; Horsley, 1978; Greenwood and Elton, 1979; Allen and Weale, 2005).

Elton and Greenwood (1970) (and Greenwood and Elton (1979)) provided a model for apostatic selection and how evidence for it might be analysed. The selection is described in terms of the relative numbers of two prey types eaten (e_1/e_2) compared to the relative numbers available (A_1/A_2). The equation for the model of frequency-dependent selection is given by:

$$e_1 / e_2 = (VA_1 / A_2)^b$$

The letter ‘b’ is for the measure of strength of frequency-dependence and the letter ‘V’ (visibility) is a measure of the frequency-independent factors such as the relative crypsis of the morphs, or colour preferences of the predators. When a range of prey populations comprising different values of A_1 / A_2 are exposed to the predators and corresponding values of e_1 / e_2 obtained, then the parameters b and V may be estimated by regression analysis (after transforming both ratios to logs) or by non-linear least squares method.

Manly proposed in 1972, 1973 and 1974 the use of the Beta (β) parameter to measure selection against one of the two prey types or it could be interpreted as the instantaneous per-item consumption rates of 'x' prey colour or 'y' prey colour, respectively or alternatively as the respective probabilities that a x (or y) prey colour is consumed given that it has been encountered, where encounters are defined such that per-item encounter rates are independent of prey type. β is estimated from sets of e_1 , e_2 , A_1 and A_2 values. A positive correlation between β and $A_1/A_1 + A_2$ from a series of trials indicates apostatic selection. The model of Manly assumes that β remains constant during every trial but Greenwood and Elton (1970) pointed out that this would be unlikely, because frequency-dependent selection involves the predators assessing the frequencies of prey presented and adjusting their behaviour accordingly.

I decided to use this method because of the simplicity to calculate and the simplicity to interpret and understand the results. And besides my experiments were not evolving experiments or in 'natural' situations but constant and 'artificial', therefore I thought it was a good idea to use this proven method to calculate selection.

Throughout this work I used β index of instantaneous preference (Manly, 1973, 1974, 1980; Manly *et al*, 1972). The value of Beta always ranges from 0 to 1 and if its value is 0.5 there is no selection. In most cases I measured selection against grey prey, so that if the value is over 0.5 then selection is against grey prey and if the value is under 0.5 then selection is against brown prey.

This is the equation for Beta (selection against grey prey):

$$\beta = \log (g / G) / [\log (g / G) + \log (b / B)]$$

Where: G = grey presented, g = grey not eaten, B = brown presented and b = brown not eaten.

All values of Beta were Arcsine-transformed or angular transformed, this transformation is especially appropriate to percentages and proportions (Sokal and Rohlf, 1995) to use the data in parametric analysis. The term arcsin is synonymous with inverse sine or \sin^{-1} , which stands for the angle whose sine is the given quantity. Thus, if we look up the proportion 0.431 we find 41.03° , the angle whose sine is square root of 0.431. The arcsine transformation stretches out both tails of a distribution of percentages or proportions and compresses the middle. Values after the arcsine transformation range from 0 to 90.

Chapter III

Crypsis: Do Predators Choose Unmatching Prey?

Introduction

The main aim of this series of experiments was to test the simple hypothesis that avian predators will select against unmatching prey when given the choice between matching and unmatching prey. There is substantial evidence for such behaviour (see Chapter I and Edmund 1974), but it is important to verify that such frequency independent selection occurs in the main system used in this thesis, namely pastry baits resting in a background containing apparent matching stones.

(3.1) Experiment to test crypsis with two stones densities (600 and 200 stones)

a) Aims

The aims of this experiment were (1) to test the efficacy of Cooper's (1984b) method for testing selection for crypsis in a heterogeneous background and (2) to compare the effect of using two different densities of matching stones. We predict that frequency independent selection against conspicuous prey should be stronger when the density of matching stones is higher, because the background will be more complex (with more matching elements and overall more elements to process). Therefore birds should focus their efforts more strongly on the more contrasting prey.

b) Material and methods

A hessian sheet was used as background (4 m long x 1.4 m wide) (area 5.6 m²) with four treatments, two with a high density of stones (600 stones), of which one was grey stones only and the other brown stones only, and two with a low density of stones (200 stones), of which one was grey stones only and the other brown stones only (see Chapter II). The stones were placed haphazardly (or evenly dispersed) on the hessian sheet by hand and each of the treatments was repeated 10 times in a random order (using a random number generator in my calculator) and after that the data was pooled (average) for each treatment (number and colour of stones), therefore we had 40 trials at each site and 120 trials as a whole.

All the trials were performed by me, therefore only one trial at the time was performed. When a trial was finished I moved to the next site and started another trial.

The numbers of prey presented on each background/treatment were 25 grey prey and 25 brown prey. Each trial was stopped when about half of the prey had been eaten, usually after about one hour.

c) Predators

I recorded the maximum numbers of birds seen foraging together at the same time (because is impossible to know which bird is visiting the place for a second or third time) (Table 3.1.1).

Table 3.1.1 List of birds involved in the experiments.

Species	Site 1	Site 2	Site 3
Magpie (<i>Pica pica</i>)	1	-	-
Collared Dove (<i>Streptopelia decaocto</i>)	2	-	4
Starling (<i>Sturnus vulgaris</i>)	1	1	-
Robin (<i>Erithacus rubecula</i>)	1	-	4
Carrion Crow (<i>Corvus corone</i>)	-	2	2
Blackbird (<i>Turdus merula</i>)	-	5	2

d) Pre - training

The birds were trained to feed by throwing handfuls of ‘white’ baits over hessian sheets placed on each of the experiment sites. The training lasted for 12 days before the start of the experiments at each site.

e) Chronology

All the experiments were carried out in three sites between 9 November and 7 December 2003, starting at 07:00 each day and finishing at noon.

f) Results

i. Selection

The mean values of β (against grey) for selection in the four background treatments on three sites are shown in Table 3.1.2.

Repeated Measures ANOVA on the β (arcsine transformed) values for grey prey (Table 3.1.3) tested the main effects of crypsis, stone density (two levels, 200 and 600 stones), stone colour (two levels, brown and grey), experimental site (three levels) and their interactions. A second analysis of variance (Table 3.1.5), was on β (arcsine transformed) values for grey prey in grey backgrounds and β (arcsine transformed) for brown prey in brown backgrounds, to test whether the prey were equally cryptic in their respective matching backgrounds.

For each site, selection against grey was greater in brown stones than in grey stones, irrespective of stone density (Table 3.1.2). However, this effect was more marked in the 600 stones background (Table 3.1.2). This interaction was significant ($F= 317.06$, $p < 0.001$). All other interaction were non-significant (Table 3.1.3). In 200 stones matching probably appeared less cryptic to the birds because they had more space between them and there was more distance to the nearest stone of the same colour.

This experiment suggests that the colours of prey were a good match for the stones (Table 3.1.2). Prey with a matching colour were always less predated, especially in 600 stones backgrounds. This also agrees with reflectance spectral data for prey and stones (unpublished).

Table 3.1.2 Comparison of selection in 200 stones treatment against 600 stones treatments: mean values of $\beta \pm$ standard error. The values of β (arcsine transformed) were calculated for grey prey.

EXPERIMENT SITES	200 STONES		600 STONES	
	GREY	BROWN	GREY	BROWN
Site 1	40.79 \pm 9.50	50.70 \pm 5.67	19.62 \pm 6.34	67.25 \pm 3.48
Site 2	40.47 \pm 5.43	48.02 \pm 4.24	23.93 \pm 4.17	68.56 \pm 4.01
Site 3	42.36 \pm 4.14	50.28 \pm 4.90	24.38 \pm 5.47	68.51 \pm 4.85

Table 3.1.3 Repeated Measures ANOVA on mean values of β against grey prey (arcsine transformed) testing the effects of three factors (stone colour, density of stones in the background and experimental sites) and the interactions between them.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F	P
Stone colour	21806.968	1	21806.968	566.588	<.001
Error	346.394	9	38.488		
Stone density	.120	1	.120	.008	.931
Error	137.269	9	15.252		
Site	65.669	1.79	36.611	1.164	.332
Error	507.633	16.14	31.445		
Stone colour – Stone density interaction	10268.270	1	10268.270	317.057	<.001
Error	291.476	9	32.386		
Stone colour – site interaction	48.922	1.841	26.574	.826	.446
Error	533.127	16.569	32.176		
Stone density – site interaction	93.591	1.972	47.465	2.096	.153
Error	401.793	17.746	22.641		
Stone colour-Stone density-site interaction	2.861	1.604	1.784	.071	.896
Error	360.967	14.435	25.007		

ii. Which colour was a better match to its respective matching background?

For this Repeated Measures ANOVA, β results (arcsine transformed) were calculated for the matching prey in each treatment. In other words, β was calculated for grey when grey was resting in grey backgrounds and for brown prey when the background was brown stones (Table 3.1.5). Thus the intention was to test whether each prey colour (grey or brown) was an equal match to its respective matching background (grey or brown) as perceived by the birds.

Table 3.1.4 Comparison of selection in 200 stones treatment against 600 stones treatments: mean values of $\beta \pm$ standard errors. The values of β (arcsine transformed) were calculated for grey prey in grey stones and for brown prey in brown stones.

EXPERIMENT SITES	200 STONES		600 STONES	
	GREY	BROWN	GREY	BROWN
Site 1	40.79 \pm 9.50	39.29 \pm 5.67	19.62 \pm 6.34	22.74 \pm 3.48
Site 2	40.47 \pm 5.43	41.97 \pm 4.24	23.93 \pm 4.17	21.43 \pm 4.01
Site 3	42.36 \pm 4.14	39.71 \pm 4.90	24.38 \pm 5.47	21.48 \pm 4.85

In the analysis (Table 3.1.5), stone colour did not have a significant effect. Density alone had a significant effect over selection, which we already know. Thus the birds selected in a similar manner against unmatching prey in both grey stones and brown stones. The two kinds of prey used during the experiments thus seemed to be equally camouflaged when resting in these ‘matching’ backgrounds.

Table 3.1.5 Repeated Measures ANOVA results for testing whether the two prey colours are equally matching to the two colours of stone, using β (arcsine transformed) for grey prey when the background was grey and β for brown prey when the background was brown.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F	P
Stone colour	20.312	1	20.312	.316	.588
Error	578.894	9	64.322		
Stone density	10268.270	1	10268.270	317.057	<.0001
Error	291.476	9	32.386		
Site	48.922	1.841	26.574	.826	.446
Error	533.127	16.569	32.176		
Stone colour – Stone density interaction	.120	1	.120	.008	.931
Error	137.269	9	15.252		
Stone colour – site interaction	65.669	1.794	36.611	1.164	.332
Error	507.633	16.143	31.445		
Stone density – site interaction	2.861	1.604	1.784	.071	.896
Error	360.967	14.435	25.007		
Stone colour-Stone density-site interaction	93.591	1.972	47.465	2.096	.153
Error	401.793	17.746	22.641		

g) Discussion

This experiment supports the view that selection by wild birds on dimorphic prey in heterogeneous backgrounds is favourable to prey that are cryptic (Cott 1940, Edmunds 1974). The preferences of birds for grey or brown prey was strongly influenced by the colour and also by the density of stones in the background. Prey were at lower risk when they matched the background and the background was more complex (high density – 600 stones). I also found that both prey colours were equally camouflaged when resting in the background that corresponded to its colour (grey or brown) (Table 3.1.5).

Based on these results I decided to continue the use of Cooper's (1984b) experimental model of hessian sheets and stones throughout the rest of the work reported in this thesis, because I found good evidence that prey colour and stones colour was a good match. The design works, is easy to manipulate, and a good way to test not only crypsis but also the relationship of crypsis with a range of factors, such as background tracking (experiment 3.2), the relationship of crypsis with apostatic selection (Chapter IV) and the effect of distance to matching stones on selection (Chapter V).

(3.2) Background tracking experiment

a) Aims

The aims of this experiment were, (1) to test whether predators select against prey resting on backgrounds that make them conspicuous and, more importantly, (2) to test the hypothesis of Endler (1974) that when there are two cryptic morphs in a population and one is similar to the colour pattern of the least common colour in the background, while the other one is most similar to the most common colour pattern, then the second one will have a higher level of crypsis and thus will be better protected. Ultimately in natural population, this should result in the frequencies of the morphs becoming proportional to the frequencies of the elements of the background to which they are similar. One frequency of prey (5:5) was used because that way the frequency-dependent factor did not affect selection and the results were easier to interpret. In other words, only variation in the background had an influence in selection. Thus in this experiment different proportions of stones were used. Different densities of stones were also used, with the aim of testing whether selection against the less cryptic prey is stronger when stone densities are higher. The use of more than one density of stones represents an extension of Cooper's (1984b) work, because he used a single density of 600 stones, and is a logical progression from the experiment described in 3.1.

b) Materials and Methods

The backgrounds were hessian sheets and with the same stones (grey and brown) as in experiment 3.1. Factors used (prey frequency was constant): Stone frequency (9 levels: 1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1), Stone density (3 levels: 200, 500, 1000), Stone colour match (2 levels: matching, unmatching) (oriental red and oriental white, described in Chapter 2). In each of the 15 sites the 9 stone frequencies were presented twice at each combination of density x colour match, giving a total of $9 \times 6 \times 2 = 108$ trials per experiment and a total of $108 \times 15 = 1620$ trials in the experiment as a whole.

Within each site the order of the 108 trials was decided at random (www.random.org/nform.html). Each repetition lasted between 15 and 30 minutes.

The 15 experiment sites were situated along the riverbank of the Culiacan river in Culiacan, Sinaloa, Mexico, each separated from the nearest site by at least 1km. Two teams worked at the same time in different sites. Team A was only me and Team B was a team formed by two local biologists (personal friends). Before the actual experiment started they were trained by

me with 'training trials', that way they were familiarize with the method. Team A worked from site one to site seven and Team B worked from site eight to site 15 (experimental sites previously marked).

Baits were made in the usual manner and the same two colours, grey and brown were used (Chapter II). In this experiment 50 baits were used, presented in a frequency of 5:5 in every trial. The distribution was haphazard; handfuls were thrown from shoulder height onto the sheet, repeating the procedure for any prey that bounced off the hessian sheet or ended up resting on a stone.

Each trial was stopped when about half of the prey had been eaten.

Manly's (1973) beta index (β) (arcsine transformed) was used to measure selection against grey baits.

c) Predators

About 90 % of the predators were the great-tailed grackle (*Quiscalus mexicanus*) and the rest were house sparrows (*Passer domesticus*).

d) Pre-training

Training was not needed, because the grackle colony lives in the trees close to the experimental sites and the birds are very exploratory, checking everything in their vicinity. The colony totals around 5000 birds in an area of 20 linear kilometres along the Culiacan-Tamazula river (personal observations).

e) Chronology

All the experiments were performed in Culiacan, Sinaloa, Mexico (northwest Mexico), from 1 October 2005 to 3 March 2006.

f) Results

Results obtained were analysed as a community. They were not separated by experimental site but by treatment (1000 matching and unmatching stones, 500 matching and unmatching stones and 200 matching and unmatching stones). This way of analysing the data gives bigger samples and therefore more robust results (Dr. Patrick Doncaster, personal communication). Selective behaviour of the birds in this experiment appears to be statistically dependent on the proportions of stones (Figure 3.2.1 and Table 3.2.1). More importantly there was a significant interaction of this factor with density and colour of stones. In other words, grey prey were preferred over brown when the frequency of grey stones in the background was low, and this preference was reversed when grey stones were at a high frequency in the background. There was no such effect in non-matching backgrounds.

ANCOVA showed a significant difference between slopes (each slope represent a site) in the 1000 matching stones treatments ($F = 2.99$, $p = 0.0003$), but not in the case of 1000 unmatching stones treatments ($F = 0.968$, $p = 0.486$). In the case of the 500 matching stones treatments, there was a significant difference between slopes ($F = 1.83$, $df = 14$, $p = 0.0350$), on the other hand the 500 unmatching stones treatments showed no significant variation between sites ($F = 1.53$, $df = 14$, $p = 0.1003$). For the 200 stones treatments (both matching and unmatching) the differences were not significant. This means that only in the matching treatments at high densities (500 and 1000 stones) did the slopes show significant variation. Full ANCOVA results are presented in Table 3.2.2.

A further analysis was to compare all the possible pairs of slopes (Table 3.2.3). With this table you can clearly see what is the difference of having 200, 500 or 1000 matching or unmatching stones in the background. This way you can evaluate the effect of stone density in selection by birds.

Figure 3.2.1 Comparison of the overall results analysed as a community (without experimental site separation). β regressed on stone frequency. a) 1000 matching and unmatching stones, b) 500 matching and unmatching stones and c) 200 matching and unmatching stones. The dotted line and closed points represents matching stones treatment and the continuous line and open points the unmatching.

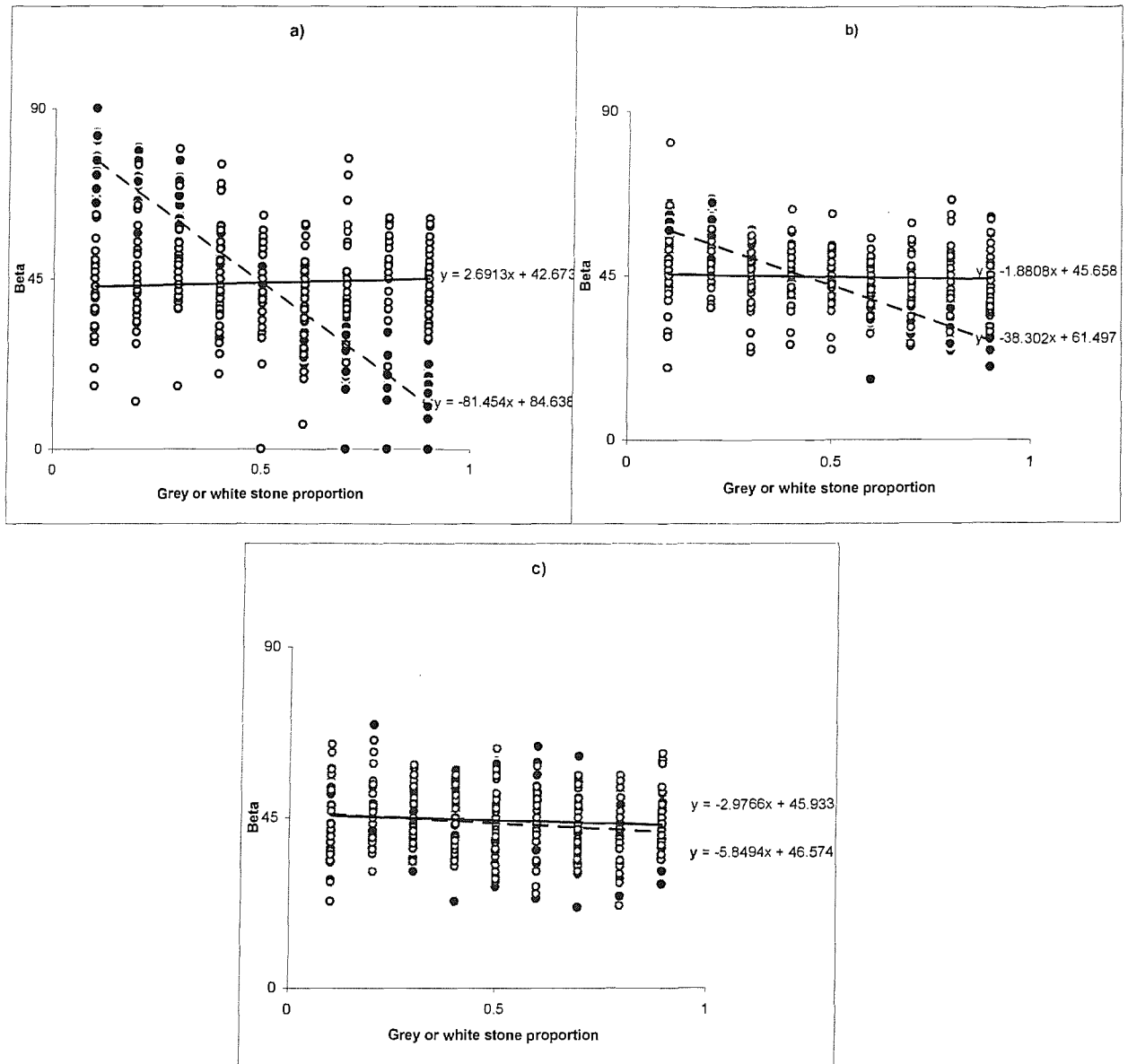


Table 3.2.1 Repeated measures analysis of variance for effects of stone proportions and the interaction with treatments (densities and colour of stones).

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F	P
Proportions	7.26	50202.050	6910.351	102.561	.0001
Treatments - Proportions	36.324	100314.119	2761.663	40.987	.0001
interaction					
Error	1264.068	85170.744	67.378		

Table 3.2.2 Analysis of covariance to compare slopes (b values) of β on stone frequency, for within each of the six treatments (15 slopes for each treatment, each slope represents an experimental site).

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F	P
1000 matching slopes	14	1567.43	111.95	2.99	.0003
Error	240	8987.21	37.44		
1000 unmatching slopes	14	1768.36	126.31	.968	.486
Error	240	31311.84	130.46		
500 matching slopes	14	569.79	40.69	1.831	.035
Error	240	5333.56	22.22		
500 unmatching slopes	14	1308.37	93.45	1.532	.1003
Error	240	14640.24	61.001		
200 matching slopes	14	322.36	23.02	.462	.9507
Error	240	11948.90	49.78		
200 unmatching slopes	14	1300.36	92.88	1.367	.1703
Error	240	16312.64	67.96		

Table 3.2.3 Pair wise comparisons (1st slope vs. 2nd slope) of the different treatments slopes (b values), with the Bonferroni Adjustment for Multiple Comparisons.

Treatments		Mean Difference	Std. Error	P	95 % Confidence interval for Difference	
1 st slope	2 nd slope				Lower Bound	Upper Bound
1 (1000 matching stones treatment)	2	-84.145	2.889	P< .001	-94.340	-73.949
	3	-43.152	3.366	P< .001	-55.034	-31.269
	4	-79.573	3.766	P< .001	-92.866	-66.280
	5	-75.604	2.327	P< .001	-83.817	-67.391
	6	-78.477	3.082	P< .001	-89.356	-67.598
2 (1000 unmatching stones treatment)	1	84.145	2.889	P< .001	73.949	94.340
	3	40.993	3.197	P< .001	29.709	52.278
	4	4.572	3.866	NS	-9.075	18.219
	5	8.541	2.924	NS	-1.781	18.862
	6	5.668	3.211	NS	-5.666	17.002
3 (500 matching stones treatment)	1	43.152	3.366	P< .001	31.269	55.034
	2	-40.993	3.197	P< .001	-52.278	-29.709
	4	-36.421	2.799	P< .001	-46.299	-26.543
	5	-32.453	2.407	P< .001	-40.950	-23.956
	6	-35.325	2.424	P< .001	-43.882	-26.768
4 (500 unmatching stones treatment)	1	79.573	3.766	P< .001	66.280	92.866
	2	-4.572	3.866	NS	-18.219	9.075
	3	36.421	2.799	P< .001	26.543	46.299
	5	3.969	2.260	NS	-4.008	11.945
	6	1.096	3.465	NS	-11.135	13.327
5 (200 matching stones treatment)	1	75.604	2.327	P< .001	67.391	83.817
	2	-8.541	2.924	NS	-18.862	1.781
	3	32.453	2.407	P< .001	23.956	40.950
	4	-3.969	2.260	NS	-11.945	4.008
	6	-2.873	2.508	NS	-11.727	5.981
6 (200 unmatching stones treatment)	1	78.477	3.082	P< .001	67.598	89.356
	2	-5.668	3.211	NS	-17.002	5.666
	3	35.325	2.424	P< .001	26.768	43.882
	4	-1.096	3.465	NS	-13.327	11.135
	5	2.873	2.508	NS	-5.981	11.727

g) Discussion

The evidence suggests that selection against grey and brown prey was strongly influenced by the proportions of grey and brown stones in the background (Figure 3.2.1). These changes in preference suggest that birds were selecting for crypsis by tending to overlook the colour that matched the most abundant stones in the background. This selective pattern can be attributed to the relative proportions of the two colour components on the background. For example, when many grey stones were in the background, grey prey were most likely to 'rest' against this colour and hence brown prey would be at greater risk. If the birds confused isolated baits with stones, then there is the possibility that masquerade also affected selection. Whatever the cause, it can be said that the morph that resembled the most common background colour element was more protected, because it was a better random sample of the background (Endler, 1978). Thus in natural proportions we would expect the frequencies of such a morph to increase until selection becomes nil.

There was a clear effect of the different background compositions. This was more obvious in the high-density treatments where the variation in selection between stone proportions was clearly more pronounced than in the low-density treatments (Table 3.2.2 and Figure 3.2.1). These results suggest that different backgrounds compositions significantly and strongly influenced selection by the predators. Since selection appears to be strongly affected by background colour composition, prey frequency should, therefore, 'track' temporal or spatial changes in background colour compositions or move to a different background.

Another important conclusion is that there was a significant interaction between the proportions of stones presented and stone density. This means that the reaction of the birds to the proportions of stones depended on the density of the stones. Selection against unmatching prey in high-density treatments was higher than in low-density treatments (Table 3.2.2).

The birds appeared to select significantly differently between experimental sites in the 500 and 1000 matching stones treatments. The analysis of covariance (Table 3.2.2) comparing the slopes for each of the 15 sites showed significant variation only for the 500 and 1000 matching stones treatments. A possible reason for this is that the birds were less able to discriminate prey from the background in the high-density-matching stones backgrounds than in the low-density and unmatching stones ones. Prey may have been less visible in the former and therefore there may have been more accidental encounters compared with 'simpler' backgrounds where birds can spot prey more easily. These accidental encounters could occur for different reasons. For example, I

noted that sometimes larger birds walked over the hessian sheet and made depressions, sometimes causing a bait to roll and therefore become obvious.

Chapter IV

Apostatic Selection on Matching Prey

Introduction

The series of experiments in chapter III concentrated on the effects of background composition on selection when brown and grey baits were presented at a single frequency. In experiment 3.2, selection was clearly influenced by the background colour composition and in the next series of experiments the work was extended to examine frequency dependent selection. A similar design was used. This time the proportions of stones were the same throughout the experiments, but the prey proportions were changed for each trial. Thus the aim was to test whether predators select cryptic polymorphic prey apostatically because if this were not true then the most cryptic form would eventually dominate populations. Endler (1978) suggested that apostatic selection would reinforce the relationship between cryptic morph frequencies and background elements frequencies and therefore help maintain the polymorphism.

Bond (1983) found evidence that three caged pigeons apostatically selected two prey types presented in a mixed stone background that made them inconspicuous and not when he used an alternative pair of prey types that did not match the background. Cooper (1984a) also found evidence that wild garden birds selected apostatically when searching for two prey types resting in a background of stones that made them inconspicuous but not when the same prey were presented in a control unmatching background.

In the first experiment of this chapter dog pellets were used as 'prey' in different proportions over soil and grass backgrounds. The dog pellets were a good match to the backgrounds (at least to human eye). The experimental square areas were 5m x 5m. In the second and third experiments of this chapter the same basic design was used of stones resting on a hessian sheet; in both cases prey were presented in different frequencies (1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1). The differences were that (a) in the second experiment prey density was higher (8.9 m^{-2}) than in the third experiment (3.5 m^{-2}) and (b) the stones were presented in different densities; during the second experiment seven different densities were used (no stones, 100, 200, 400, 600, 700 and 1000) and for the third experiment only one (1000 stones). Matching and non-matching (white and red stones) backgrounds were used throughout the chapter to test for the possibility that selection was related to the number of colours in the background irrespective of whether they matched the colours of the baits. Thus the complexity of the backgrounds varied, at least measured by the number of stones in view. Following Endler (1978) we would expect apostatic selection to increase with the complexity in the background.

In summary, the overall aims of this chapter were (a) to test whether apostatic selection was stronger when prey are resting on backgrounds that make them inconspicuous, and (b) to test whether selection is affected by the diversity of the background irrespective of crypsis. Comparison between selection on conspicuous prey and selection on cryptic prey could be used to elucidate the behavioural mechanism of apostatic selection. In order to maximise food intake predators are likely to pay attention to specific cues associated with the prey that distinguish them from the background, or in other words forming 'search images' (Dawkins, 1971; Lawrence and Allen, 1983; Bond, 1983). Such search images are more likely to be acquired for commonly encountered morphs, hence apostatic selection. If the experiments fail to reveal apostatic selection we may then have to introduce other mechanisms to explain how the birds detect cryptic prey; for example, by decreasing their rate of search (Guilford and Dawkins, 1987).

(4.1) Dog Pellets Experiment: Testing for Apostatic Selection

a) Aims

The aim of this experiment was to test whether ground-feeding birds select apostatically on cryptic polymorphic prey resting over natural backgrounds (grass or soil) under trees near their colonies in Culiacan, Sinaloa, Mexico. It was meant as a test of a possible method of exploring frequency-dependent selection and background matching, namely using prey that matched readily available natural backgrounds (soil and grass).

b) Materials and Methods

Purina ‘Dog Chow’ dog pellets were used as prey and were presented in two colours, ‘green’ and ‘brown’. The dog pellets were spherical and of 1 cm in diameter.

A total of 50 prey were presented in 9 frequencies, ranging from 1:9 to 9:1 (1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1). These frequencies were repeated 10 times (the results were pooled for each frequency, in other words, I calculated an average for each frequency) and presented at each site in a random order. Eight sites were used in total. In total we had $9 \times 10 = 90$ trials at each site and $90 \times 8 = 720$ trials as a whole.

The eight sites were situated on the northwest bank of the Culiacan River, home to a large colony of Great-tailed grackle (*Quiscalus mexicanus*). The terrain is varied, with large patches of grass and soil. First, the eight sites were chosen on the basis of availability of both backgrounds (grass and soil). Each area was then marked into 50 m x 50 m squares (with four 50 m ropes), deliberately including into each squares the two kinds of backgrounds. After the first plot was marked we (me and two local biologists) moved upstream 500 m and started to look for the next plot. If after 500 m there was no suitable area including the two backgrounds we continued to move upstream until we found such a site. Therefore all experimental sites were at least 500 m apart from each other. Inside each 50 m x 50 m square two (one over grass and one over soil) smaller areas (5m long x 1.5m wide) were marked. Thus each site had two background treatments. In short, 16 experiments were carried out.

c) Predators

Approximately 95% of the predators were great-tailed grackle (*Quiscalus mexicanus*), and some were house sparrows (*Passer domesticus*) and black-necked stilts (*Himantopus mexicanus*).

d) Pre-training

Since the birds were used to feeding in the area, no training was required.

e) Chronology

The series of experiments were carried out from December 5 2002 to January 20 2003.

f) Results

Figure 4.1.1 gives, for each background (with no experimental site separation), β (arcsine transformed) for green prey plotted against frequency of green prey available. The positive slopes indicate apostatic selection (soil slope: $F = 120.714$, $df = 1$, error $df = 70$, $P < .0001$ and the grass slope: $F = 57.745$, $df = 1$, error $df = 70$, $P < .0001$). Comparing the two gradients, the slope for soil was steeper than the slope for grass (because selection was stronger against green prey on soil), which means apostatic selection was significantly stronger on the soil backgrounds than on the grass backgrounds ($t = 2.13$, $df = 140$, $p = .025$) (Table 4.1.1).

Using SPSS 12, a Repeated Measures ANOVA test was used to test the effects of background treatment, and sites. There was a significant effect of background treatment (soil or grass), telling us that the birds selected differently in each of the backgrounds ($F = 19.376$, $df = 1$, error $df = 8$, $P = .002$). The effect of site was not significant ($F = 2.058$, $df = 7$, error $df = 56$, $P = .167$), implying that birds selected roughly in the same way at each of the eight sites. The interaction between treatments and sites was also not significant ($F = .935$, $df = 7$, error $df = 56$, $P = .436$) (Table 4.1.2).

Figure 4.1.1 Regression of arcsine-transformed values of β (against green prey) on frequency of green prey. Dotted line and closed circles, 8 experiment on soil. Full line and open circles, 8 experiment on grass.

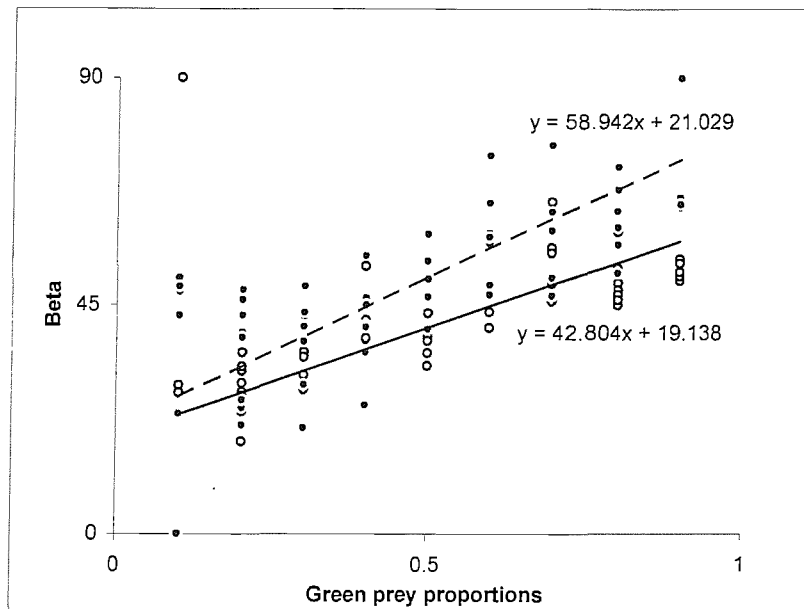


Table 4.1.1 Statistical analysis of regression lines in figure 4.1.1. T- test comparing the two slopes.

Soil Treatment Slope	Grass Treatment Slope	t	P
$58.942x + 21.029$	$42.804x + 19.138$	2.13	.025

Table 4.1.2 Repeated Measures ANOVA, for the effects of the two background treatments, the eight experimental sites and the interaction between the two factors.

Source	Sum of Squares	df	Mean Square	F	P
Background treatments	3571.176	1	3571.176	19.376	.002
Error	1474.458	8	184.307		
Sites	2646.002	7	378.000	2.058	.063
Error	10283.429	56	183.633		
Background treatments – Site interaction	557.124	7	79.589	.935	.487
Error	4767.480	56	85.134		

g) Discussion

Apostatic selection was detected in the two matching backgrounds, soil and grass. These results are similar to other results obtained with conspicuous prey (Manly *et al*, 1972; Cook and Miller, 1977; Fullick and Greenwood, 1979; Cooper, 1984b). Apostatic selection was significantly higher on the soil backgrounds than in the grass backgrounds (Figure 4.1.1 and Table 4.1.1). The apostatic selection on the soil backgrounds was perhaps higher because both pellet colours were in some way more cryptic overall (brown pellets were obviously more cryptic) on soil backgrounds than on grass backgrounds where green was a much better match to the background than the brown pellets (at least to human eye). This result is in agreement with those of Bond (1983), Cooper (1984b) and Tucker & Allen (1988), all of whom showed that apostatic selection was stronger when the prey resembles the background.

Figure 4.1.1 also indicates frequency-independent selection, because the regression line for selection against green on the soil background is consistently higher than the regression line for the grass background, implying that the green pellets were more inconspicuous on grass than on soil.

The results also showed that there was no significant variation of selection between sites (is worth to mention that the difference was very close to be significant) (Table 4.1.1). This may have been because most of the predators belonged to the same species. However, the system of soil and grass as the backgrounds severely limits the exploitation of the relationship between selection for crypsis and frequency dependence.

That is why for the next experiments the stones and hessian sheet model was used. These provide more standard and controlled conditions for the baits.

(4.2) Experiment to test for apostatic selection using the stones and hessian sheet model

Cooper (1984b) found that wild birds selected two types of prey apostatically when presented in a background composed of a hessian sheet and a single density of 600 matching stones that made them inconspicuous. The question that I tried to answer with this experiment was, “is there an influence of the density of the stones on selection?” And if the answer was ‘yes’, then is apostatic selection stronger at higher densities of stones? We might expect it should be, because the increase in the number of matching stones should make the prey more difficult to detect and hence search images should be stronger for the more commonly encounter prey.

The Cooper (1984b) model was used with a range of seven different stones densities (including no stones), with the aim of testing whether apostatic selection is increasingly stronger as the complexity of the background increases. The treatment of no stones in the background was used as a control experiment (in addition to the non-matching stones treatments) because I wanted to test whether frequency-dependent selection happens even when there are very low elements of complexity on the background.

a) Aim

The main aim of this experiment was to test whether apostatic selection increases when a range of frequencies of prey are presented in a background of a high density of matching stones.

b) Materials and Methods

The pastry prey were made in the usual manner (see Chapter II).

At each site 9 prey frequencies (1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1) were presented once in each of the 13 treatments (see Table 4.2.1), giving $9 \times 13 = 117$ trials per site and a total of $117 \times 13 = 1521$ trials in the experiment as a whole.

I used the same size of hessian sheet as in the experiments described in Chapter II & III and the same stones as used in the Chapter III experiments. The matching colours were again grey and

brown and the unmatching stones were red and white (as described in Chapter II and used in the experiments in Chapter III).

At each of the 13 sites there were 13 treatments: no stones and the 12 combinations of stone density (100, 200, 400, 600, 700, 1000) x stone colour match (matching, unmatching). The order of the treatments of stones was decided by a coin toss after finishing each trial. I randomised the stones by mixing the two colours of the stones in a bucket and then scattering them haphazardly over the hessian sheet by hand.

The distribution of the prey was also haphazard and determined by dropping handfuls of prey from shoulder height, and repeating the procedure if a prey bounced out of the hessian sheet or came to rest on top of a stone. Trials were stopped when about half of the prey had been eaten. In all the trials the numbers and species of birds were recorded and the duration of each trial and the weather conditions were noted.

The experiment used 13 experimental sites. Five were in the Southampton area in England and eight were in Culiacan, Sinaloa, Mexico (Table 4.2.1).

Within each site the order of the 117 trials was decided at random. In England each repetition last from one to four hours and in Mexico each repetition lasted between 20 and 40 minutes.

In England only one site at the time was used and in Mexico two teams worked at different sites at the same time. In Mexico the same two teams worked in this experiment as in experiment 3.2 (Team A and Team B).

c) Predators

The species and maximum numbers of birds observed feeding are listed in Table 4.2.1.

Table 4.2.1 List of predators observed in each of the experimental sites.

Species	Site 1 (UK)	Site 2 (UK)	Site 3 (UK)	Site 4 (UK)	Site 5 (UK)	Site 6 to 13 (MEX)
Magpie (<i>Pica pica</i>)	-	2	-	-	-	-
Collared Dove (<i>Streptopelia decaocto</i>)	4	-	-	-	2	-
Starling (<i>Sturnus vulgaris</i>)	3	-	2	3	-	-
Robin (<i>Erithacus rubecula</i>)	1	-	3	3	-	-
Carrion Crow (<i>Corvus corone</i>)	-	2	-	-	-	-
Blackbird (<i>Turdus merula</i>)	4	1	2	3	2	-
Rock Dove (<i>Columbia livia</i>)	2	5	1	2	2	-
Great-tailed Grackle (<i>Quiscalus mexicanus</i>)	-	-	-	-	-	* > 25
Black-Necked Stilt (<i>Himantopus mexicanus</i>)	-	-	-	-	-	* > 10

* Estimated numbers due to high number of individuals.

d) Pre - training

No training was required for the Mexican sites. For the English sites handfuls of ‘white’ pastry baits were thrown over the hessian sheet for 10 days before the start of the experiment proper.

e) Chronology

The experiment was carried out in different phases: (1) 16 February to 17 March 2004 (Southampton, England), (2) 29 March to 15 April 2004 (Culiacan, Mexico), (3) 14 December 2004 to 6 January 2005 (Culiacan, Mexico), (4) 11 March to 5 of May 2005 (Southampton, England) and (5) during the month of July 2005 (Culiacan, Mexico).

f) Results

The results were analysed as a community. They were not separated by experimental sites but separated by treatment alone (no stones, 100 matching and unmatching stones, 200 matching and unmatching stones, 400 matching and unmatching stones, 600 matching and unmatching stones, 700 matching and unmatching stones, and 1000 matching and unmatching stones). This way of analysing the data gave us bigger samples and therefore meaningful results. Experimental sites were only included as a factor in the analysis of variance (Table 4.2.3).

For each of the 13 treatments, selection against grey was estimated by use of β (Manly, 1973), arcsine transformed and regressed on prey frequency. I then performed analysis of covariance (ANCOVA) (Sokal and Rohlf, 1995) (in BIOMSTAT) to determine whether the gradients were

significantly different from one other. An analysis of variance (repeated measures in SPSS 12.0) tested whether there was a significant effect caused by the different treatments presented to the birds.

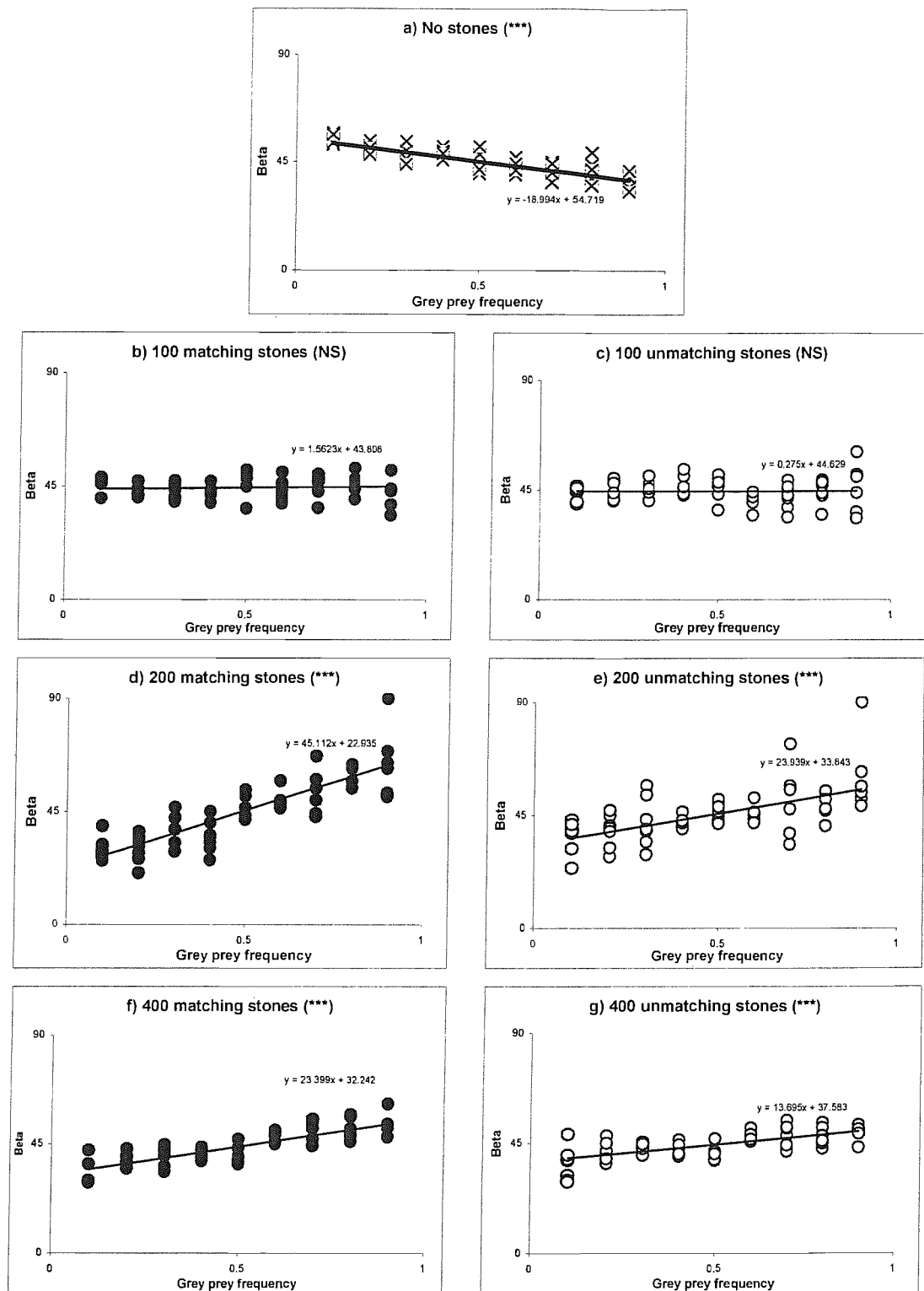
The results for the 13 treatments are shown graphically in Figure 4.2.1. With the 'no stones' treatment the birds selected in anti-apostatic fashion. In other words, they tended to concentrate on the rare form and overlook the common form, a process that will lead to extinction of the rare form (that is, the population becomes monomorphic). This anti-apostatic selection might be related to the density of the prey, perhaps because the rare prey are more conspicuous in a background of the common (Allen and Anderson, 1984). But this changed when the stones were introduced (matching or unmatching); the tendency was for selection to become apostatic (Figure 4.2.1). The only case when selection did not differ significantly from the 'no stones' treatment was with the 100 unmatching stones treatment (Table 4.2.2).

In all treatments involving stones (Figure 4.2.1) the regression lines of β on frequency are positive, suggesting that selection was apostatic. This tendency was common (and very similar) to both countries (Mexico and UK). The gradients of the lines were in a progressive order from the no stones treatment to the 1000 matching stones treatment, except for the case of the 600 and 700 matching stones (in this case the gradients were equal) and in the case of the 400 and 200 matching stones treatment, where the lower density (200) was higher than the high density treatment (400) (Figure 4.2.1 and 4.2.2).

Thus the strength of selection against the common form tended to be directly related to the density of stones. This is an important result because I found the same pattern in two very different and distant countries, with totally different species of birds. Such a pattern strongly suggests that there is a general behavioural tendency for ground-feeding birds to select against common form in heterogeneous backgrounds. ANCOVA (Sokal and Rohlf, 1995) shows that all the gradients were significantly different from each other and a more detailed comparison between pairs of treatments (control experiment included) is presented in Table 4.2.2.

The analysis of variance shows that there is a significant relationship between selection and frequency ($P < 0.001$). The analysis also showed that there is a significant difference ($P < 0.001$) between all the stone treatments. There was no significant difference between sites (full results presented on Table 4.2.3). In other words, selection was strongly affected by the composition of the background and also by the frequency of prey presented, but not by experimental site.

Figure 4.2.1 Regression of β (arcsine transformed) (for selection against grey) on frequency of grey, incorporating data from all 13 sites in Mexico and UK. Significance of gradient from zero: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ and NS not significant.



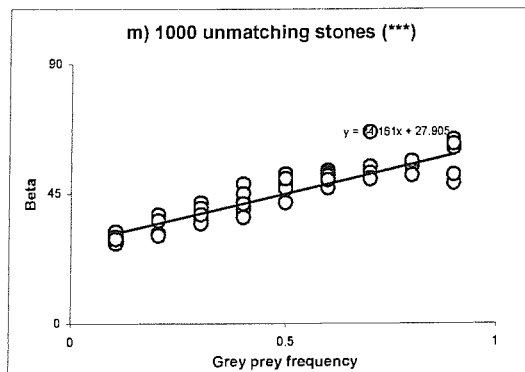
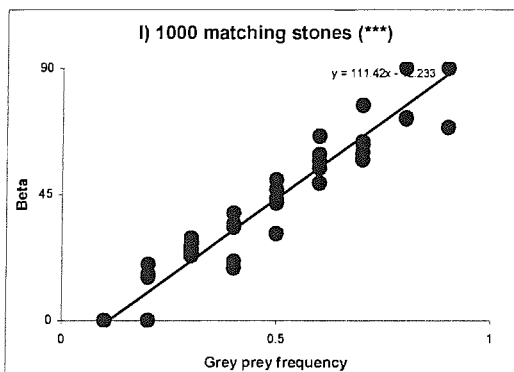
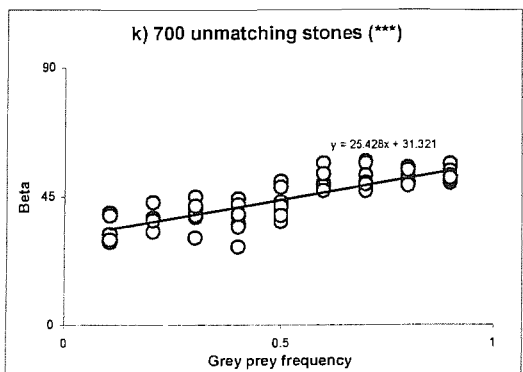
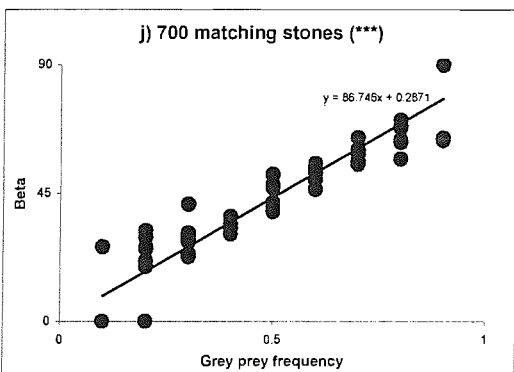
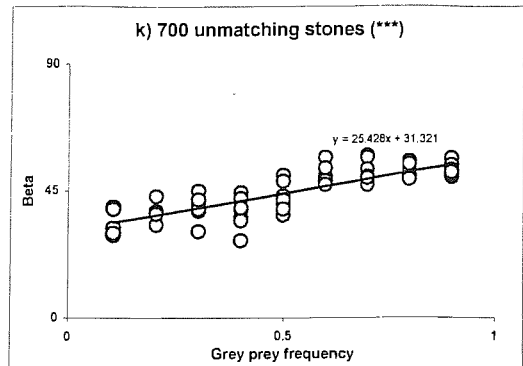
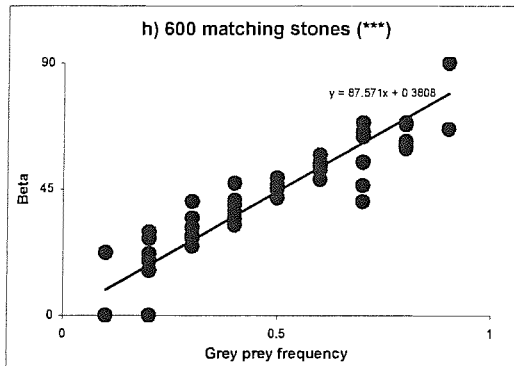


Figure 4.2.2 Summary of regression lines for data from all 13 sites in Mexico and UK: a) experiment slopes and b) control experiment slopes (the 600 slope overlaps the 700 slope). In all cases β was calculated for grey prey.

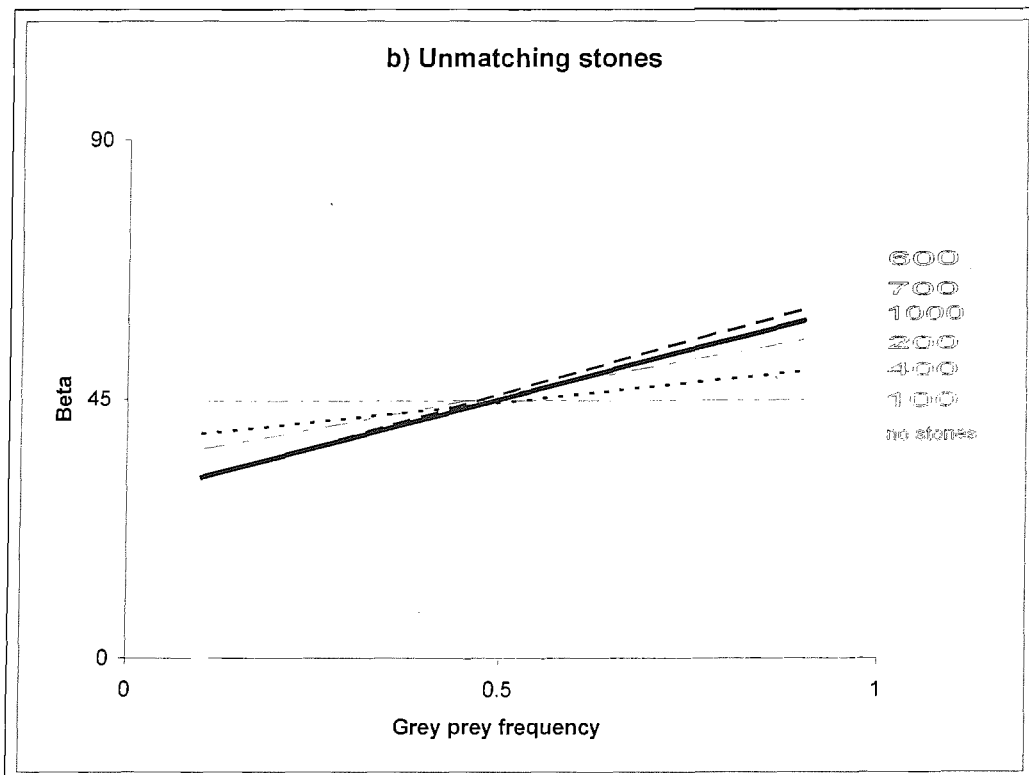
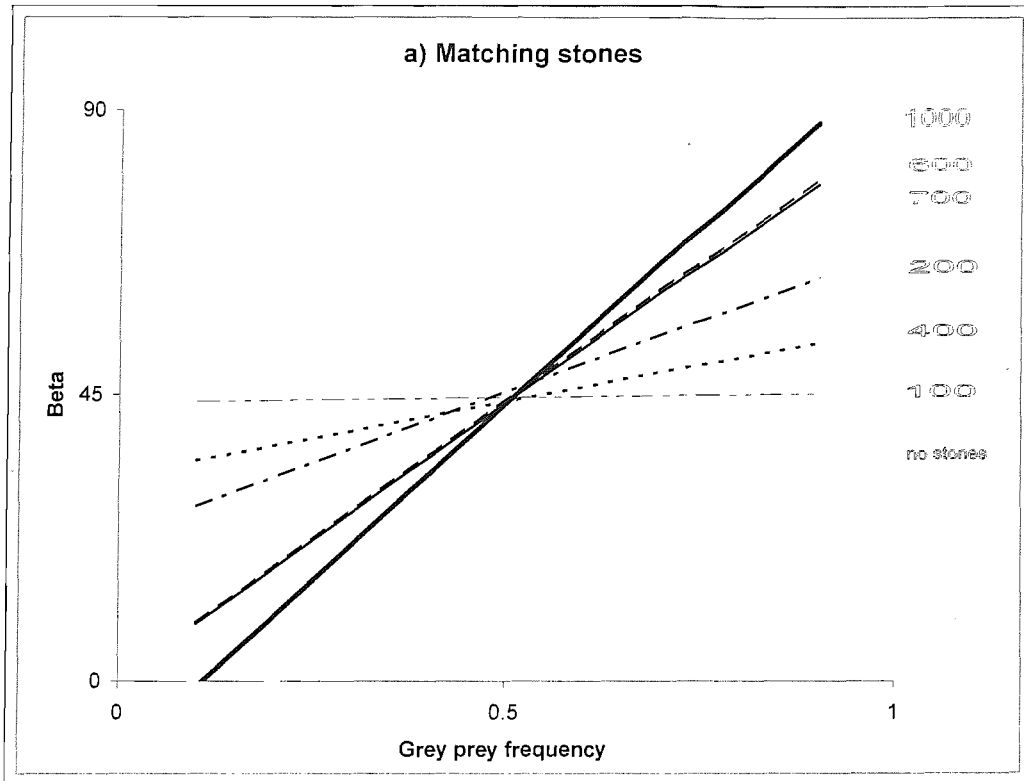


Table 4.2.2 Pair wise comparisons of gradients of regression lines (b values) for no stones against all stone treatments and matching and unmatching stones at the same density, with Bonferroni Adjustment for Multiple Comparisons.

Treatments		Mean Difference	Standard Error	P	95% confidence interval for difference	
1 st treatment of pair	2 nd treatment of pair				Lower bound	Upper bound
1 (no stones slope)	2	-20.556	2.568	.016	-37.200	-3.912
	3	-19.269	3.273	NS	-40.485	1.947
	4	-57.909	6.264	.007	-98.506	-17.313
	5	-40.135	5.445	.025	-75.427	-4.842
	6	-42.393	2.201	.001	-56.656	-28.130
	7	-32.689	2.971	.003	-51.942	-13.436
	8	-99.426	10.097	.005	-164.870	-33.982
	9	-52.230	4.228	.001	-79.630	-24.830
	10	-105.740	4.717	.001	-136.311	-75.169
	11	-44.422	3.433	.001	-66.673	-22.172
	12	-130.411	3.960	.001	-156.076	-104.746
	13	-53.155	3.149	.001	-73.562	-32.748
	2 (100 matching stones slope)	3 (100 unmatching stones slope)	1.287	2.862	NS	-17.259
4 (200 matching stones slope)	5 (200 unmatching stones slope)	17.774	7.625	NS	-31.648	67.196
6 (400 matching stones slope)	7 (400 unmatching stones slope)	9.704	2.902	NS	-9.108	28.515
8 (600 matching stones slope)	9 (600 unmatching stones slope)	47.196	9.127	NS	-11.958	106.350
10 (700 matching stones slope)	11 (700 unmatching stones slope)	61.318	5.952	.004	22.743	99.893
12 (1000 matching stones slope)	13 (1000 unmatching stones slope)	77.256	4.707	.001	46.750	107.763

Table 4.2.3 Analysis of Variance (Repeated Measures) for effect of the 13 stone treatments and for the experimental sites.

Source	Sum of Squares		Mean Squares		
		df	F	P	
Treatments	116976.026	12	9748.002	71.600	.001
Error	9802.476	72	136.146		
Sites	1612.083	13	124.006	1.482	NS
Error	13056.431	156	83.695		

g) Discussion

When the birds were presented with a ‘simple’ background with no stones, selection was anti-apostatic. In other words, the birds concentrated their attacks against the rare form (Figure 4.2.1a). This results supports the findings of other workers (Allen and Clarke, 1968; Greenwood, 1969; Allen, 1972; Allen, 1976; Cook and Miller, 1977; Horsley, 1979; Willis *et al.*, 1980; Allen and Anderson 1984; Allen *et al.*, 1998; Allen and Weale 2005). In these cases birds concentrated disproportionately on the rare forms when presented with prey populations at high densities (from 8 per square metre to more than 10,000). There are at least two possible explanations for the results in the current experiment: (1) without the ‘interference’ from the stones the birds’ perception was different so they perceived the prey to be at high density, with the rare form having a higher contrast in the ‘sea’ of common forms, (2) to avoid a monotonous diet (Greenwood, 1984; Allen, 1989).

Where the two colours of prey matched their background there is good evidence that the predators selected against the common form; therefore selection was apostatic in most densities of stones (Clarke 1962) (Figure 4.2.1). In other words, the risk of the common colour being eaten increased as prey frequency and the density of matching stones increased. The slopes for matching stones were progressively higher as the stone density increased (except for the case of 400 and 200 stones, where the 200 treatment slope was higher) (Figure 4.2.2a). Why was there stronger apostatic selection when there were higher densities of stones in the background? One possible reason is that the increased number of matching elements made the prey more cryptic, forcing the bird to adopt stronger search images, and this will be most likely for the more commonly encountered colour (Tinbergen, 1960; Dawkins, 1971a, 1971b; Mueller, 1971; Reid and Shettleworth, 1992; Langley, 1996). In the case of the ‘unmatching stones’ treatments the slopes also followed a progressive trend as stones density increased, but these gradients were not as steep and the rankings were not as

clear as in the ‘matching stones’ treatments (the 600 and 700 slopes overlapped and were higher than the 1000 slope) (Figure 4.2.2b). This is an interesting result, because the birds appeared to select against the common form even on the backgrounds where prey were conspicuous. The selection was not as strong as in the matching backgrounds but nevertheless rare prey tended to be protected.

At low densities of matching stones such as 100, selection was the same as in 100 unmatching stones. In the case of 200 matching stones apostatic selection had the same strength as in 200 and 400 unmatching stones. This could mean that the cryptic effect of stones starts to increase the strength of apostatic selection only after a certain threshold density. Before this the apostatic selection is generated by the presence of stones, whether matching or non-matching. The stones presumably make the prey more difficult to find (anachoresis, Edmunds (1974)) and ‘force’ the birds to concentrate on searching common prey. The addition of stones at increasing densities effectively reduces the density of the prey. Indeed, other experiment in which the actual density of conspicuous prey is altered suggests that apostatic selection is inversely correlated with density (Weale *et al*, 2000) as originally predicted by Clarke (1962).

The results covered two countries with different species and completely different conditions (habitat, weather, etc.). For example, in Mexico the conditions were more ‘natural’, because birds were less influenced by human activity than the birds in England where the birds were those commonly found in home gardens. Even with all these differences selection had the same pattern, which is strong evidence for a general tendency for ground-feeding birds to feed apostatically in complex backgrounds. Different sites did not have a significant effect on selection by birds in the two countries (Table 4.2.3).

(4.3) Experiment to test for apostatic selection at low densities of prey

Past experiments have found evidence that selection by birds (captive quail) is affected by the density of prey presented, becoming strongly apostatic when the densities are low (1.25 to 2.5 baits m^{-2}) and progressively weaker at higher densities (5 to 7.5 baits m^{-2}) (Cook and Miller, 1977). Other experiments using pastry baits also found that wild birds select apostatically when presented at low densities (2 baits m^{-2}) and anti-apostatic when presented with high densities ($>10,000$ baits m^{-2}) (Allen and Clarke, 1968; Allen, 1972; Allen, 1976; Horsley *et al.*, 1979; Allen *et al.*, 1998; Weale *et al.*, 2000). What would happen to selection if the density of prey in the experiments described in 4.2 was reduced further?

a) Aims

To test whether apostatic in a single high stone density background selection becomes stronger when prey densities are lower (3.5 baits m^{-2}) than in the past experiment (experiment 4.2) where a prey density of 8.9 m^{-2} was used.

b) Materials and Methods

The pastry prey was made in the usual manner (Chapter II).

I used nine different frequencies of 20 prey in each of two backgrounds (1000 matching stones and 1000 unmatching stones). The nine possible frequencies (1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1) were used one time, in other words, we had $2 \times 9 = 18$ trials at each experimental site and $18 \times 15 = 270$ trials for the experiment as a whole. All frequencies were presented in a random order at each of the 15 sites, determined by a random number generator (www.random.org/nform.html).

The distribution of the prey was haphazard, determined by dropping handfuls of prey from shoulder height, repeating the procedure if a prey bounced out of the hessian sheet or came to rest on top of a stone. Trials were stopped when about half of the prey had been eaten.

I used the same hessian sheet as in the other experiments (Chapter III and experiment 4.2 of Chapter IV) and the same stones (same size as in the 4.2 experiment of Chapter IV) with the same two colours (grey and brown) and a series of control experiment with red and white stones (the same used in the experiments in Chapter III and in experiment 4.2 of Chapter IV).

Two treatments of stones were used: 1000 matching stones and 1000 unmatching stones. The order of the treatments of stones was decided by a coin toss after finishing each trial. The stones were randomised by mixing the two colours of the stones in a bucket and then scattering them haphazardly over the hessian sheet by hand.

Again in this experiment two teams (Team A and Tema B) as in experiment 4.2 worked at the same time in different sites. Team A (me) in the first 7 sites and Team B (two local biologists) in the last 8 sites.

In all the trials the numbers and species of birds were recorded and the duration of each trial and the weather conditions were noted.

c) Predators

Again 90% (approx) were from the species *Quiscalus mexicanus* and the rest were *Passer domesticus* (home sparrows).

d) Pre - training

No pre-training was needed because the birds were used to feeding in the area of the experimental sites.

e) Chronology

The experiments were carried out during the months of February and March of 2006 in Culiacan, Sinaloa, Mexico.

f) Results

Selection was apostatic when the prey were on both matching and non-matching stones. In both cases the regression of β on prey frequency was positive (Figure 4.3.1). Analysis of variance results showed a significant difference between the two treatments (1000 matching and 1000 unmatching stones) (Table 4.3.1). The analysis of covariance shows that slopes for the two treatments were significantly different, with a steeper slope when the prey were inconspicuous (Table 4.3.2). This is evidence that when prey are resting in a background that makes them inconspicuous apostatic selection will be stronger.

A comparison between the slopes for 1000 stones with 50 prey in experiment 4.2 (Figure 4.2.1c and m) and the slopes for 1000 stones with 20 prey of this experiment revealed significant differences (Figure 4.3.2, Table 4.3.3). In the case of matching stones, apostatic selection was stronger with 50 prey than 20 prey which contradicts the theory that says that apostatic selection will be stronger at low density. In the second comparison between the unmatched stone treatments apostatic selection was stronger for the lower density of prey (Table 4.3.3, Figure 4.3.2).

Figure 4.3.1 Comparison between regression for β (arcsine transformed) on grey prey frequency for 1000 matching stones treatment (continuous line) and 1000 unmatched stones treatment (dotted line).

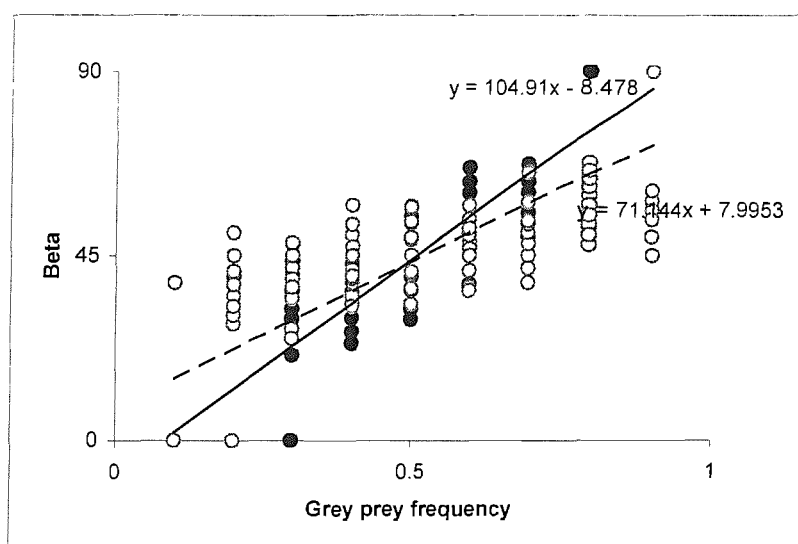


Table 4.3.1 Summary of ANOVA Repeated Measures, for the effect of stone treatment.

Source	Sum of Squares	df	Mean Square	F	P
Stone treatments	7593.647	1	7593.647	60.520	P < 0.001
Error	1756.628	14	125.473		

Table 4.3.2 Analysis of Covariance for the difference between gradients of the regression lines in Figure 4.3.1.

Source	df	Sum of Squares	Mean Square	F	P
Matching					
vs.	1	9112.3742	9112.3742	73.855	P < 0.001
Unmatching					
Error	536	66133.0173	123.3825		

Figure 4.3.2 a) Comparison between regression of β on prey frequency for 20 prey in a 1000 matching background and 50 prey in a 1000 matching background. b) Comparison between regression of beta on prey frequency for 20 prey in a 1000 unmatching background and 50 prey in a 1000 unmatching background. The broken lines are for high density and continuous lines are for low density. Filled circles for the high-density treatments and the empty circles for the low-density treatments.

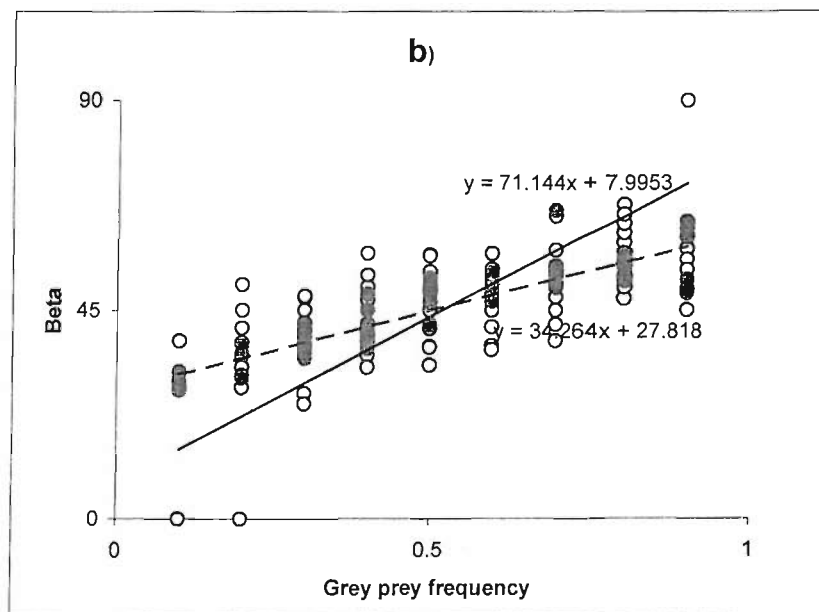
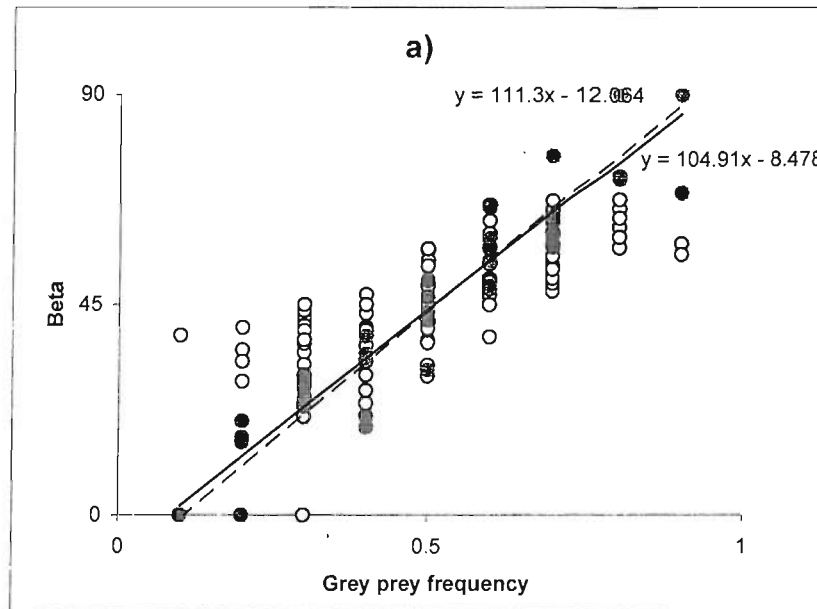


Table 4.3.3 Summary of Analysis of Covariance for differences among slopes in Figure 4.3.2 (a and b)).

Source	df	Sum of Squares	Mean Square	F	P
1000matching-50 prey vs. 1000matching-20 prey.	1	367.0235	367.0235	4.637	.0317
Error	536	42426.2050	79.1533		
1000unmatching- 50 prey vs. 1000unmatching- 20 prey.	1	12240.9031	12240.9031	156.274	P= 0.001
Error	536	41984.8091	78.3298		

g) Discussion

Selection in both treatments (matching and unmatching backgrounds) was apostatic. Apostatic selection was stronger when prey was presented on backgrounds that made them inconspicuous. But the interesting results is that when this slope (20 prey presented over a 1000 matching background) was compared against the slope of 50 prey presented over a 1000 matching stones background in experiment 4.2 the difference was statistically significant over the 20 prey slope (Figure 4.3.2 and Table 4.3.3). This contradicts the results obtained elsewhere (Allen and Clarke 1968, Allen 1972, Allen 1976, Cook and Miller 1977, Horsley et al. 1979, Allen and Anderson 1984) which supported the prediction that apostatic selection will be stronger if prey were presented in lower densities (Clarke, 1962). On the other hand, when the slope for 20 prey over 1000 unmatching stones background was compared against the slope of 50 prey presented over 1000 unmatching stones background, the low prey density treatment was significantly higher (Figure 4.3.2 and Table 4.3.3). These results agree with the general trend of previous experiments (Allen and Clarke 1968, Allen 1972, Allen 1976, Cook and Miller 1977, Horsley et al. 1979, Allen and Anderson 1984).

Clearly more work is needed. However, a possible explanation for the apparent discrepancy when the stones were matching is that the stones generate some kind of 'interference' in birds' perception and therefore prey density was perceived to be roughly the same in both treatments (20 prey and 50 prey).

Chapter V

Physical Protection: Are Pastry Prey Safer When Close To Stones?

Introduction

So far, we have focused on two different interacting factors that are possibly affecting selection by birds hunting by sight: crypsis and frequency dependent selection. Additional factors may be anachoresis (hiding) and masquerade. Because there are more stones, the prey may have been more difficult to find simply because they tend to be more hidden from the visual field of the birds (anachoresis). For example since the birds forage at ground level their field of vision will often be obstructed by stones and they will only see the prey in front of the stones. Indirect evidence for such an effect comes from the finding of apostatic selection even in backgrounds of unmatching stones (Chapter IV), suggesting that the birds were 'forced' to concentrate more on common prey when their prey were hard to find because they 'hid' amongst the stones (because the probability to find a common form not hidden is higher than finding a rare form not hidden, therefore easier to form a search image). Another possible factor is that the prey sometimes resemble small stones (masquerade). However, this is difficult to test and is not discussed here.

The only work that I found about this subject is that of Cooper (1984b). In his experiments he took colour photographs of the backgrounds before and after each trial. He found that resting close to matching stones did not seem to offer any protection and therefore concluded 'this result suggests that the birds did not detect or overlook the prey as a result of matching comparisons between prey items and neighbouring stones at the local level of the area around each stone' (Cooper, 1984b. Pages: 214-217). Cooper's experiment was the basis of the next set of experiments. This time, to simplify the design and interpretation, I designed experiments in which the prey was positioned deliberately close to matching or unmatching stones, thus making it easier to judge the effect of physical protection offered by inanimate objects.

(5.1) Experiment with one stone colour in the background with one prey of one colour resting close to the stones and the others scattered among the stones.

For this experiment only one colour of stones was used for the background treatments, in order to provide a homogeneous background to the prey, simplifying the interpretation of the results. For example, prey resting close to matching stones are expected to be more protected than unmatching prey resting far from the stones. The design also will tell us whether prey resting close to unmatching stones are more or less protected than the matching prey far from the stones. In addition the experiment should tell us whether resting close to stones offers the prey protection regardless of the colour (anachoresis).

a) Aims

The aim of this experiment was to test whether the prey are more protected from predation when positioned close to a stone of the same colour, as predicted from our understanding of the evolution of crypsis.

b) Materials and Methods

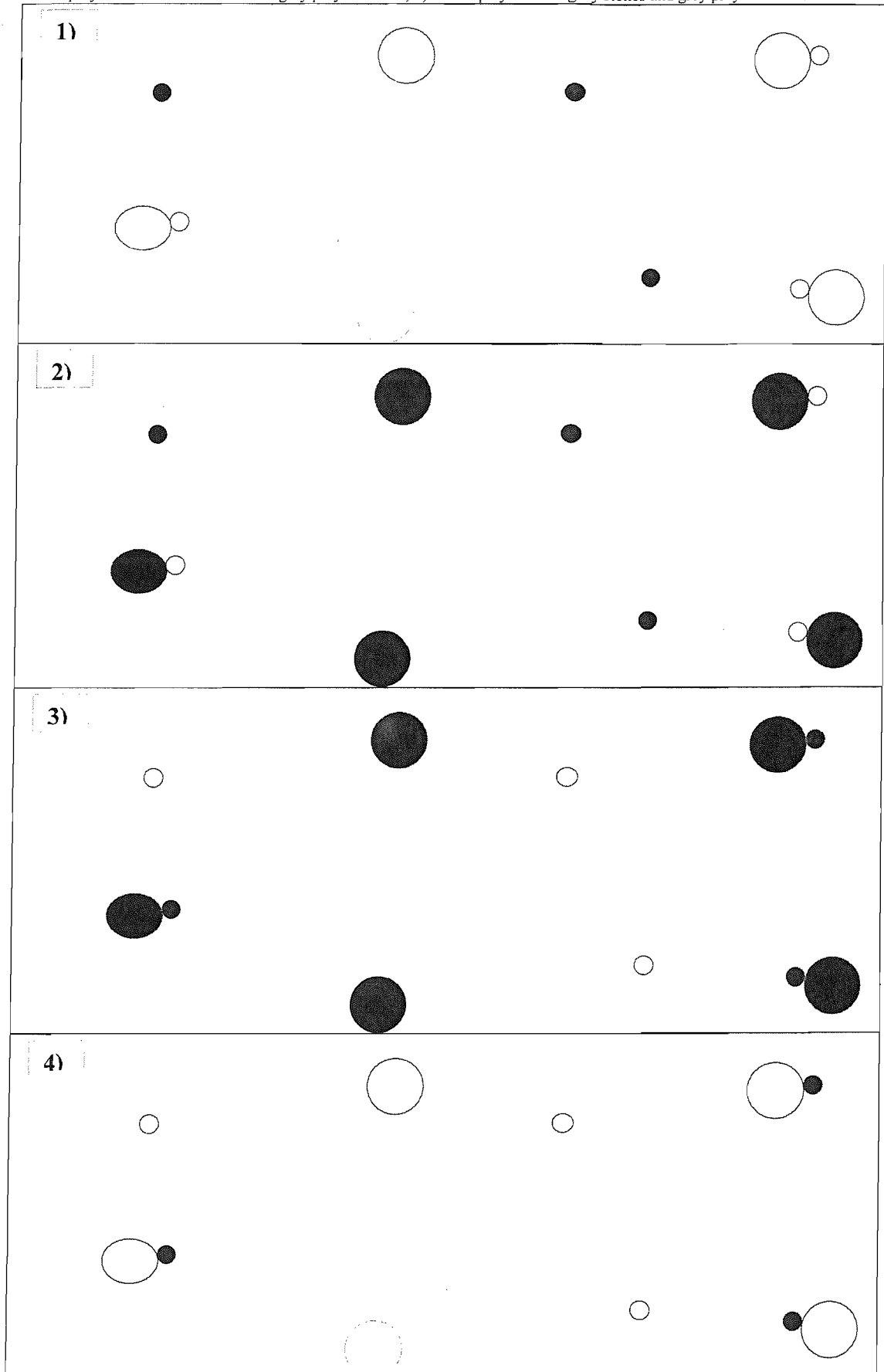
For the background the same hessian sheet and stones were used as in the past experiments (Chapter II, III and IV). The stone background was composed of 600 stones of one colour alone (grey or brown). The stones were distributed haphazardly by throwing handfuls onto the sheet so that the whole sheet appeared to be evenly covered.

The pastry prey were made in the usual manner (Chapter II), 25 grey prey and 25 brown prey were presented in every trial, with one of the colours resting close to the stones (placed deliberately to touch the stones) and the other distributed haphazardly in between the stones by throwing handfuls from shoulder height over the backgrounds, repeating the throw for any prey that came to rest over or touching the stones.

Four treatments repeated 10 times each were used in each of the four sites ($4 \times 10 = 40$ trials at each site and $40 \times 4 = 160$ trials for the experiment as a whole). They were presented at random using a random number generator (www.random.org/nform.html): (1) grey prey close to grey stones, (2) grey prey close to brown stones, (3) brown prey close to brown stones and (4) brown prey close to grey stones. Figure 5.1.1 may help the reader to visualize these treatments.

Trials were stopped when half of the prey had been eaten.

Figure 5.1.1 Schematic examples of the experimental treatments, 1) grey prey (empty small circles) close to grey stones (empty big circles) and brown prey (filled small circles) scattered, 2) grey prey close to brown stones (filled big circles) and brown prey scattered, 3) brown prey close to brown stones and grey prey scattered, 4) brown prey close to grey stones and grey prey scattered.



c) Predators

A list of species is presented in Table 5.1.1.

Table 5.1.1 List of predators (with estimated numbers) observed in each of the experimental sites.

Species	Site 1	Site 2	Site 3	Site 4
Magpie (<i>Pica pica</i>)	-	4	-	-
Collared Dove (<i>Streptopelia decaocto</i>)	2	-	-	-
Starling (<i>Sturnus vulgaris</i>)	2	-	2	3
Robin (<i>Erithacus rubecula</i>)	1	-	2	2
Carrion Crow (<i>Corvus corone</i>)	-	2	-	-
Blackbird (<i>Turdus merula</i>)	3	1	2	5
Rock Dove (<i>Columbia livia</i>)	-	4	1	2

d) Pre - training

Birds were trained to associate the experimental sites with food availability by throwing handfuls of undyed pastry baits over the hessian sheets for seven days before the start of the experiment at each site.

e) Chronology

The experiment was carried from 4 May 2004 to 10 June 2004. The four sites were in gardens around Southampton, England. Each trial started at 8:00 and finished until half of the prey had been eaten.

f) Results

The data show that for each of the eight pairs of means, prey resting close (touching) to stones (whether matching or unmatching) have statistically significantly more protection than those further away from the stones, irrespective of whether the prey close to the stones were matching or not (Table 5.1.2.). Thus in a background of brown stones, grey prey were at a greater risk when scattered than close, and the same applies to grey prey in a background of grey stones.

Selection consistently departed from random for all four treatments (Table 5.1.4).

Analysis of variance (repeated measures) showed significant main effects of distance from stone, stone colour and site (Table 5.1.4). However, there were also significant interactions between distance from stone and stone colour, and site and stone colour (Table 5.1.2 and 5.1.3). Thus the prey were more protected when close to stones and this protection was enhanced when they matched the colour of the stones, but this effect varied with stone colour, suggesting that the match between prey and stone colour was different for grey and brown. Also the effect of stone colour varied among sites.

To test whether there was a difference in the match of each prey colour to its respective stone colour a pair wise comparison (adjustment for multiple comparisons: Bonferroni) was carried out on β values for grey prey when grey was resting close to stones (grey or brown) and for brown prey when brown prey was resting close to stones (grey or brown). The full results are given in Table 5.1.5.

Table 5.1.2 Mean values of β (arcsine transformed) for grey prey close to matching stones and close to unmatching stones for all four sites.

Colour of Stone			Grey prey scattered \pm SE	Grey prey close \pm SE
	Sites			
Brown	1		52.90 \pm 5.49	41.23 \pm 4.60
	2		60.70 \pm 5.63	42.64 \pm 3.95
	3		61.09 \pm 4.83	44.28 \pm 4.52
	4		58.84 \pm 4.49	42.35 \pm 3.53
Grey	1		42.17 \pm 4.90	29.25 \pm 5.02
	2		46.90 \pm 3.71	34.15 \pm 8.79
	3		41.40 \pm 3.41	31.73 \pm 5.13
	4		43.25 \pm 3.84	29.04 \pm 3.54

Table 5.1.3 Analysis of variance (repeated measures) on β against grey prey for the effects of distance (prey close or scattered), stone colour, sites and the interaction between them.

Source	Sum of Squares	df	Mean Square	F	P
Distance	7920.079	1	7920.079	421.631	.0001
Error	169.059	9	18.784		
Stone colour	7045.420	1	7045.420	152.039	.0001
Error	417.057	9	46.340		
Sites	477.353	3	159.118	5.978	.003
Error	718.621	27	26.616		
Distance x					
Stone colour	113.750	1	113.750	18.532	.002
Error	55.243	9	6.138		
Distance x					
Sites	72.531	3	24.177	1.031	.395
Error	633.177	27	23.451		
Stone colour x					
Sites	176.895	3	58.965	3.866	.020
Error	411.781	27	15.251		
Distance x					
Stone colour x	101.148	3	33.716	1.298	.295
Sites					
Error	701.411	27	25.978		

Table 5.1.4 A t-test comparing all results of beta (β) against 45 or no selection. All β values were calculated for selection against grey prey.

β Mean Value +/- SE	β expected on the basis of random predation	t (df = 39)	P
Grey prey scattered in			
brown stones 58.39 +/- 5.94 n= 40	45	14.24	.0001
Grey prey close in brown stones			
42.63 +/- 4.16 n= 40	45	-3.596	.0005
Grey prey scattered in grey stones			
43.43 +/- 4.40 n= 40	45	-2.251	.0272
Grey prey close in grey stones			
31.0481 +/- 6.091 n= 40	45	-14.49	.0001

Table 5.1.5 Pair wise comparisons using Bonferroni adjustment for multiple comparisons, using β values for grey prey when grey was resting close to stones (grey or brown) and for brown prey when brown prey was resting close to stones (grey or brown).

Treatments		Mean Difference	Standard Error	P	95% Confidence Interval for Difference	
1 st treatment of the pair	2 nd treatment of the pair				Lower Bound	Upper Bound
1 (brown close to brown)	2	-14.958	1.041	.0001	-17.851	-12.065
	3	-11.019	1.292	.0001	-14.611	-7.427
	4	0.566	1.441	NS	-3.440	4.572
2 (brown close to grey)	3	3.939	.986	.002	1.199	6.679
	4	15.524	1.253	.0001	12.043	19.006
3 (grey close to brown)	4 (Grey close to grey)	11.585	1.143	.0001	8.408	14.762

g) Discussion

The results showed that resting close to stones offers protection to the prey irrespective of colour. This result contradicts the results obtained by Cooper (1984) when he found that birds never overlooked a prey if it was resting close to an unmatching or matching stone, perhaps because his prey never rested close enough to the stones for the stone to exert some kind of protection over the prey. The protection offered by stones is perhaps caused because ground-feeding birds standing on the hessian have their view of prey blocked by the stones (anachoresis).

The analysis of variance showed that distance to the stones had a significant effect in predation, implying that resting close to the stones offers protection independently of the other factors. However, the interaction between distance (close or scattered) and stone colour was significant, telling us that the birds were influenced by the distance of prey to the stones interacting with the colour of the prey and the stones in the background. In other words, prey were also more protected when resting close to matching stones than when resting close to unmatching stones and scattered among the stones (Table 5.1.3). The effect of the colour of the stones in the background was significant as well. Thus crypsis also played an important role during predation. In other words when a prey rested in a matching stones background more protection was offered irrespective of the distance. The experimental sites also had a significant effect which is not an uncommon finding (Allen, 1976 and other experiments in this thesis).

(5.2) Experiment to test the effect of proximity of prey to stones in a frequency-dependent design

From the results of the last experiment, if prey are more protected resting close to matching elements then, could this factor affect the strength of apostatic selection?

a) Aims

The main aims of this experiment were (1) to test whether prey resting close to matching stones are more protected than those resting close to unmatching stones and (2) to test the interaction of this factor with frequency dependent selection.

b) Materials and Methods

Prey were made in the usual manner, with the same two colours as before (grey and brown) (Chapter II).

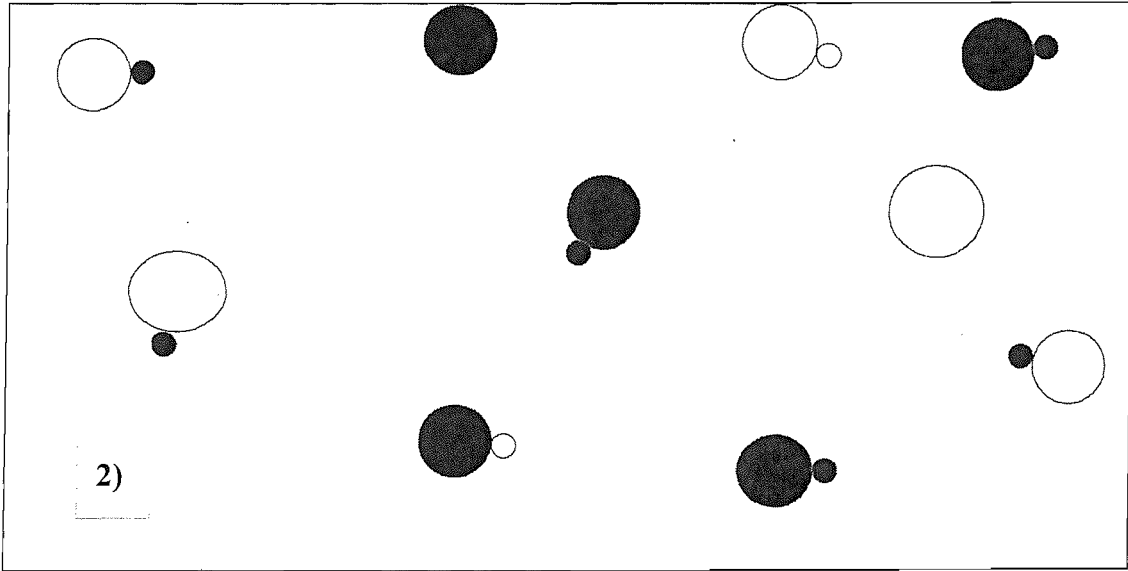
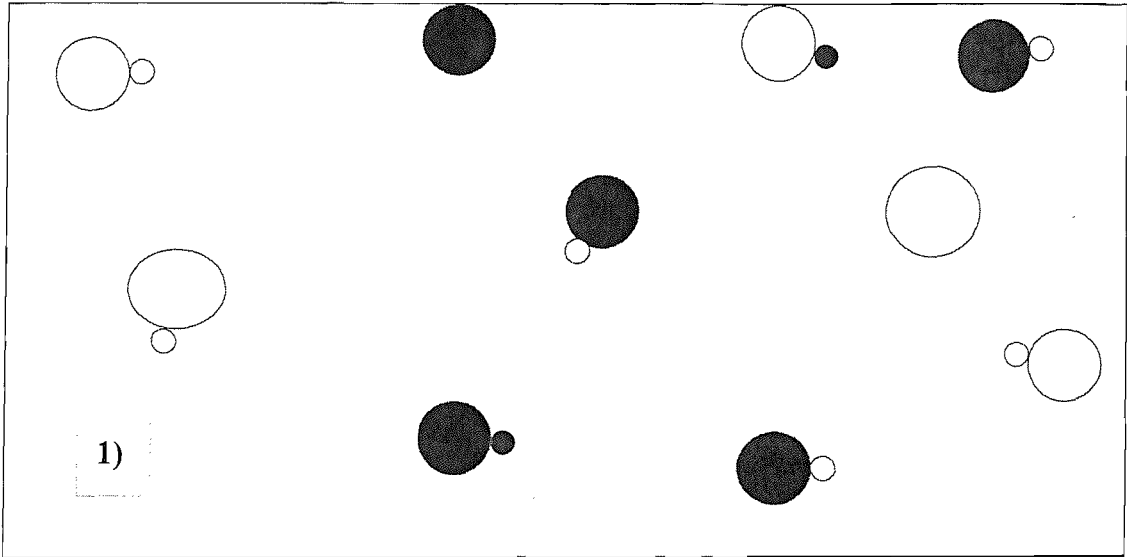
The background was the usual hessian with the usual stones (grey and brown), 50% grey and 50% brown of 600 stones (Chapter II).

Only two prey frequencies were used: 40 grey, 10 brown and 10 grey, 40 brown. Handfuls of prey in the appropriate proportions were dropped from shoulder height and then every prey was placed close to the nearest stone where it landed. First two groups of 25 prey (20 of the common and 5 of the rare) were counted and labelled as 'prey close to matching stones' and 'prey close to unmatching stones'. The first group of baits ('prey close to matching stones') were then thrown over the hessian sheet and then each one was adjusted to touch the nearest matching stone. The same was done for the second group of baits ('prey close to unmatching stones') only this time the baits were moved to touch the nearest unmatching stones. Thus of the 50 prey, half the common prey were near to matching stones and half the rare prey were near to matching stones. The rest were near to unmatching stones (Figure 5.2.1).

Ten trials for each prey frequency treatment were performed in every site (10 x 2 = 20 trials at each site and 20 x 3 = 60 trials in the experiment as a whole) and each trial was stopped when roughly half of the prey had been eaten.

All the trials were performed by me, performing ten trials (at random) in each site and after that I moved to next site (a coin toss decided to which site I was going to move to).

Figure 5.2.1 Schematic examples of both treatments, 1) half of common grey prey (empty small circles) close to grey stones (empty big circles) and the other half of grey prey close to brown stones (filled big circles). Half of rare brown prey (small filled circles) close to matching stones (filled big circles) and half close to unmatching stones (empty big circles), 2) the same arrangement as in the first treatment, only with the prey frequencies inverted (brown prey common and grey prey rare).



c) Predators

The species and estimated numbers are listed in Table 5.2.1.

Table 5.2.1 List of predators (and estimated maximum numbers) observed in each of the experimental sites.

Species	Site 1	Site 2	Site 3
Magpie (<i>Pica pica</i>)	1	-	-
Collared Dove (<i>Streptopelia decaocto</i>)	-	-	-
Starling (<i>Sturnus vulgaris</i>)	-	2	1
Robin (<i>Erithacus rubecula</i>)	-	1	2
Carrion Crow (<i>Corvus corone</i>)	1	-	-
Blackbird (<i>Turdus merula</i>)	1	2	4
Rock Dove (<i>Columbia livia</i>)	4	1	2

d) Pre - training

To train the birds to feed, handfuls of white (or undyed) pastry baits were thrown over the hessian sheets, maintaining a constant supply every day for 7 days.

e) Chronology

The experiment started on 17 June 2004 and ended on 7 July 2004. Trials started at 08:00 am and ended at 16:00 pm.

f) Results

Manly's β (arcsine transformed) was used to measure the overall risk to grey prey (Table 5.2.2). Analysis of variance (repeated measures) (Table 5.2.3) showed that selection was affected significantly by prey frequency ($F = 38.139$, $P < 0.0001$), confirming that overall selection was apostatic. There was no significant variation among sites ($F = .183$, $P = 0.834$).

Table 5.2.2 Mean β (\pm standard error) values for overall selection against grey prey.

Sites	Beta (β)	
	10 grey – 40 brown	40 grey – 10 brown
1	37.26 \pm 5.57	56.13 \pm 3.77
2	27.77 \pm 13.49	61.15 \pm 15.76
3	36.61 \pm 16.70	52.69 \pm 9.14

Table 5.2.3 Summary of analysis of variance (repeated measures) for the effects of frequency (grey prey common or rare) and site.

Source	Sum of Squares	df	Mean Square	F	P
Frequency	7783.072	1	7783.072	38.139	.0001
Error	1836.636	9	204.071		
Sites	61.351	2	30.675	.183	.834
Error	3018.612	18	167.701		

To test the prediction that overall apostatic selection could be caused by the greater number of common prey resting near to unmatching stones, a comparison was made between the risk to rare and common prey resting close to matching stones. For this, two values for beta were calculated for each prey colour; (1) β for grey prey rare resting close to grey stone, (2) β for grey prey common resting close to grey stone, (3) β for brown prey rare close to brown stones and (4) β for brown prey common close to brown stone. Full comparisons in Table 5.2.3. Analysis of variance was then used to test for the effect of frequency (rare or common resting close to matching stones), colour (prey colour, to see if one colour was a better match for its respective matching stone), experimental sites and the interaction between them. None of the results were significant (Table 5.2.5). Thus it appears that selection on prey next to matching stones was unaffected by whether the colour was rare or common.

The mean values of β were all below 45, suggesting that the colour did indeed match the background. This is confirmed by the analysis in Table 5.2.6. The difference from 45 was statistically significant for grey prey, whether rare or common. Selection against brown near to brown stones was not statistically significant; suggesting again that the match of brown prey to brown stones is not as close as the match of grey prey to grey stones.

Table 5.2.4 Mean β values (\pm standard error) for each of the two prey colours (grey prey and brown prey) when close to matching stones β for grey when rare, β for grey when common, β for brown rare, β for brown when common.

Stones	Prey Frequency	
	Rare (close)	Common (close)
Grey	34.12 \pm 27.83	41.68 \pm 7.47
Brown	36.09 \pm 25.43	42.78 \pm 7.57

Table 5.2.5 Summary of analysis of variance (repeated measures) for the effects frequency (rare or common prey), colour (prey colour), experimental sites and the interaction between them. The beta values (arcsine transformed) used for this analysis are for each prey colour. For grey prey: (1) beta for grey prey rare and (2) beta for grey prey common. And for brown prey: (1) beta for brown prey rare and (2) beta for brown prey common.

Source	Sum of Squares	df	Mean Square	F	P
Frequency	1522.584	1	1522.584	2.658	.137
Error	5154.858	9	572.762		
Colour	70.320	1	70.320	.458	.516
Error	1383.254	9	153.695		
Sites	2602.744	2	1301.372	3.082	.071
Error	7599.926	18	422.218		
Freq x Col	5.754	1	5.754	.058	.815
Error	892.790	9	99.199		
Freq x Sites	819.555	2	409.777	1.354	.283
Error	5449.413	18	302.745		
Col x Sites	176.048	2	88.024	.264	.771
Error	5991.242	18	332.847		
Freq x Col x sites	1954.953	2	977.476	2.486	.111
Error	7076.220	18	393.123		

Table 5.2.6 A t-test comparing all results of beta (β) against 45 or no selection.

β Mean Value +/- SE	β expected on the basis of random predation	t (df = 58)	P
Grey rare - grey stone 34.12 \pm 27.83	45	2.14	.036
Grey common - grey stone 41.68 \pm 7.47	45	2.38	.020
Brown rare - brown stone 36.09 \pm 25.43	45	1.918	.06
Brown common - brown stone 42.78 \pm 7.57	45	1.604	.114

g) Discussion

What was very clear in this experiment is that for the overall data frequency had a significant effect on selection, with the birds selecting against the common form and overlooking the rare ones (Table 5.2.1 and 5.2.2). The effect of the experimental sites in the experiment was not significant, suggesting that birds selected roughly in the same manner across all sites (Table 5.2.1).

The results were in the direction predicted from the hypothesis that rare prey resting close to matching stones should be more protected but they did not receive statistically significant higher protection than common prey resting close to matching stones (Table 5.2.3, 5.2.4 and 5.2.5). There was no significant effect of any of the main factors involved or in any of the interactions. In other words across all experimental conditions selection was roughly the same.

The comparison of the results against 45 (or no selection) showed that selection against grey prey was significantly different from 45. In the case of brown prey, selection was not significantly different from 'no selection', implying that grey prey were a better match to grey stones (Table 5.2.2).

From this experiment, we can conclude that the effect of prey resting close to matching elements is not a main factor contributing to apostatic selection. By implication, it is the overall relationship between prey frequency and the background that is important. However, more work is needed in

the subject of prey proximity to matching elements to have a better understanding of its importance in frequency dependent selection.

(5.3) Experiment with one stone colour in the background and one prey colour (50% close to stones and 50% scattered)

This experiment had a simple design. A single colour of stones was used and likewise a single colour of prey, half of which were close to the stones and half away from the stones.

a) Aims

The aims of this experiment were (1) to test whether prey resting close to matching stones are more protected than prey scattered that also match the background and (2) to test whether stones offer protection to prey irrespective of colour.

b) Materials and Methods

In this experiment pastry baits were again used, manufactured in the usual manner (Chapter II).

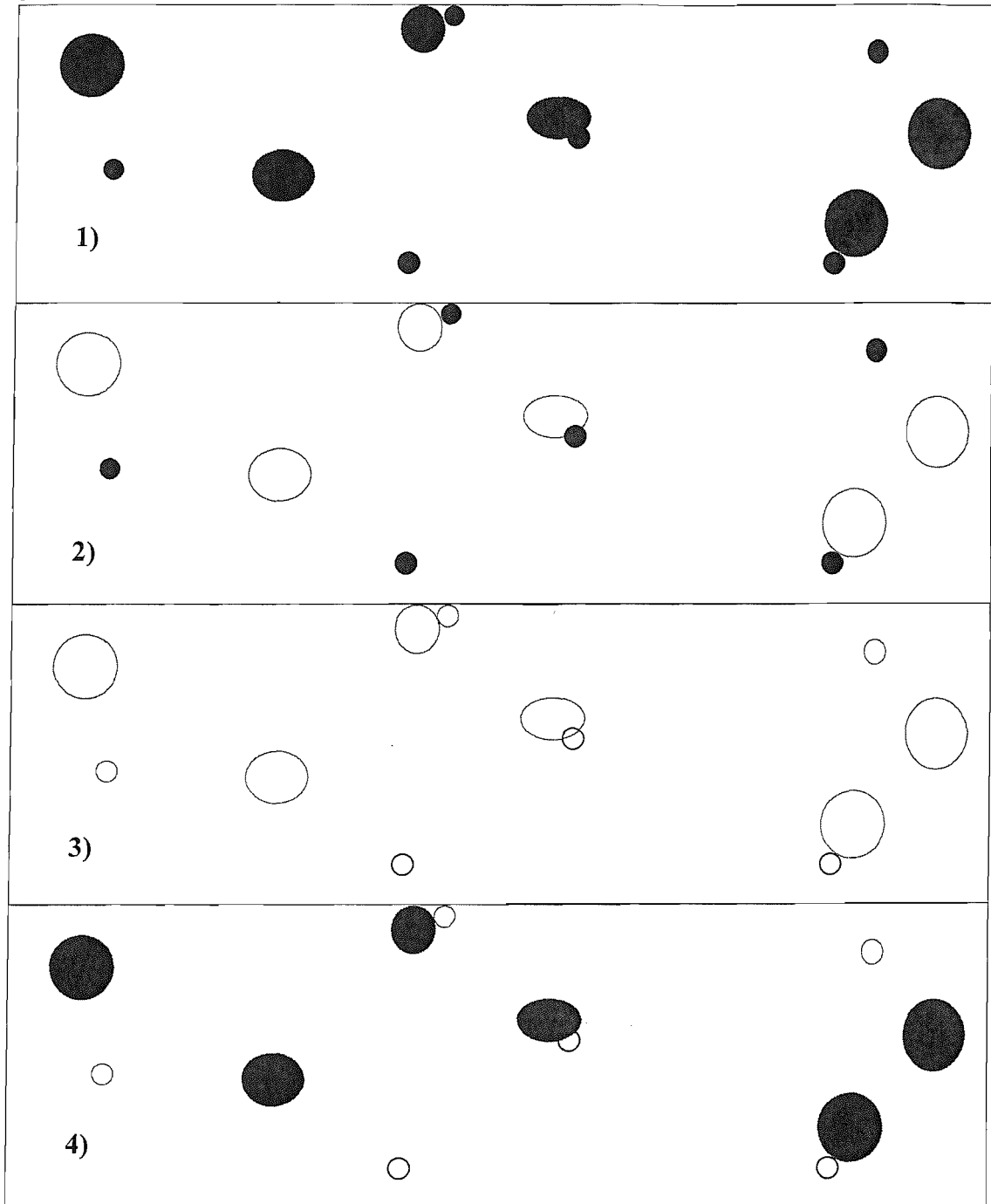
The model of stones and hessian sheets used during this thesis and during Cooper's (1984b) work was again used, this time with 600 stones of one colour alone (grey or brown).

The same colours of prey used in past experiments were used (grey and brown). 50 prey of the same colour were presented with 25 close to stones and 25 scattered. The 25 prey resting close to stones were placed haphazardly by throwing handfuls from shoulder height over the backgrounds, and then depending where the prey landed, each one was moved to the nearest stone. The remaining 25 prey were scattered haphazardly (or evenly disperse) among the stones.

Four possible treatments were used: (1) brown prey in brown stones background, (2) brown prey in grey stones background, (3) grey prey in grey stones background and (4) grey prey in brown stones background. Every treatment was repeated 10 times in each of the four experimental sites around the Southampton (UK) area.

Every trial was stopped when roughly half of the prey had been eaten.

Figure 5.3.1 Schematic example of the four treatments, (1) half of brown prey (filled small circles) close to brown stones (filled big circles) and the other half of brown prey scattered, (2) half of brown prey close to grey stones (empty big circles) and the other half scattered, (3) half of grey prey (empty small circles) close to grey stones and the other half scattered and (4) half of grey prey close to brown stones and the other half scattered.



c) Predators

The species of predators seen are listed in Table 5.3.1, along with the estimated maximum numbers of each.

Table 5.3.1 List of predators, with maximum numbers observed in each of the experimental sites.

Species	Site 1	Site 2	Site 3	Site 4
Magpie (<i>Pica pica</i>)	-	4	-	-
Starling (<i>Sturnus vulgaris</i>)	2	-	2	3
Robin (<i>Erithacus rubecula</i>)	3	2	-	3
Carrion Crow (<i>Corvus corone</i>)	-	1	-	-
Blackbird (<i>Turdus merula</i>)	3	3	2	4
Rock Dove (<i>Columbia livia</i>)	-	-	-	2

d) Pre - training

Training was carried out throwing handfuls of white undyed baits (and sometimes pieces of bread) over the hessian sheets without stones for 10 days before the experiments.

e) Chronology

This experiment was carried out from 10 August 2004 to 15 September 2004. The experiments started at about 9:00 and finished at about 16:00.

f) Results

Manly's β was calculated for prey resting close to stones and then a t-test was applied to test whether there was a significant difference between selection against prey resting close to (touching) matching stones and prey resting close to unmatching stones. An analysis of variance (Repeated measures) was carried out to test the impact on selection of the combination of prey and stones in the background (matching or unmatching), the distances of prey to the stones (close and scattered), the experimental sites and the interaction of the factors stone colour with prey colour. A summary of these results is presented on Table 5.3.3. Selection against prey resting close to matching stones was not significantly different from selection against prey resting close to unmatching stones. None of the other factors or their interaction had a significant effect. These results tells us that prey were more protected resting close to the stones irrespective of colour than the prey scattered among matching stones. Full results are presented in Table 5.3.2.

An extra comparison of the results against 45 (no selection) was carried out to test whether resting close to the stones offers significant protection. Selection was not at random and resting close to the stones actually lowers the risk of predation, irrespective of whether or not the prey matches the stones in colour (Table 5.3.4).

Figure 5.3.2 Mean values of β (\pm standard error) for prey resting close to matching stones and close to unmatching stones.

Prey	Stones	
	Grey	Brown
Grey close	37.53 \pm 8.05	36.66 \pm 6.43
Brown close	36.16 \pm 9.07	36.18 \pm 7.91

Table 5.3.3 Summary of analysis of variance (repeated measures) for the effects of prey colour, stone colour, experimental site and the interaction between the factors prey colour and stone colour.

Source	Sum of Squares	df	Mean Square	F	P
Prey colour	34.395	1	34.395	.565	.471
Error	547.940	9	60.882		
Stone colour	7.135	1	7.135	.154	.704
Error	416.809	9	46.312		
Sites	153.051	3	51.017	.719	.550
Error	19163.942	27	70.998		
StonexPrey	8.013	1	8.013	.241	.636
Error	299.746	9	33.305		

Table 5.3.4 A t-test comparing mean values of β (\pm standard error) against 45 (no selection).

β Mean Value \pm SE	β expected on the basis of random predation	T (df = 78)	P
Grey prey - grey stone 37.53 \pm 8.05	45	5.858	.0001
Grey prey - brown stone 36.66 \pm 6.43	45	8.194	.0001
Brown prey - brown stone 36.18 \pm 7.91	45	7.033	.0001
Brown prey - grey stone 36.16 \pm 9.07	45	6.158	.0001

g) Discussion

Prey resting close to matching stones were no more protected than prey resting close to unmatching stones (Table 5.3.2). Comparing the results of this experiment with the past two experiments (5.1 and 5.2) I conclude that prey were more protected resting close to stones irrespective of colour only in frequency-independent conditions, because in the experiment 5.2 results showed that selection was mainly influenced by the frequency of the prey and not where the prey was resting (close or scattered). This was probably caused by the fact that birds acquire 'search images' for the more common form in the frequency-dependent situations (experiment 5.2) and when prey were presented in the same proportions in different positions (close to stones or scattered among stones) birds did not see the prey close to stones (masquerade or anachoresis) and therefore found more often the scattered ones.

Other evidence supporting the idea that prey are more protected resting close to unanimated or inedible objects are the results obtained in the analysis of variance where the interaction of stone colour and prey colour was clearly not significant. This effect tells us that any combination of prey-stone used had the same effect regardless of which of the two treatments (prey that match the stones and prey that do not match the stones) was presented (Table 5.3.3).

It seems that physical protection was the deciding factor in selection in these series of experiments. If this is true in natural situations (not controlled experiments such as mine) then maybe prey species are not always looking for a background which they match but also look for protective objects for anachoresis. One reason why no significant effect of crypsis was detected could be that the birds easily acquired search images for matching prey of a single colour, perhaps by encountering the scattered individuals first.

Chapter VI

Final Discussion

In this final chapter I will try to put together the main points made in the past chapters. I will discuss the importance of the findings and the extent to which they achieved the aims established in Chapter I. Thus I will try to explain (1) whether a cryptic prey is more protected than a conspicuous one, (2) the occurrence of stronger apostatic selection when prey are inconspicuous compared to when conspicuous, (3) how the complexity of the background affects the strength of apostatic selection, (4) the protection offered by stones to prey resting close to them and (5) the general trends in two completely different countries (UK and Mexico).

(6.1) To What Extent Were The Aims Achieved?

a) Crypsis

Support for the widely accepted hypothesis that prey are safer when resting in matching backgrounds that make them inconspicuous is presented in Chapter III (Experiment 3.1, 3.2), where birds were presented with prey on backgrounds that made them conspicuous and inconspicuous when prey frequency was kept constant. The results showed statistically significant selection against prey that are in unmatching backgrounds and are in general agreement with classic experiments on, for example, moths and snails as summarized by Edmunds (1974).

In experiment 3.1 the design was very simple, with two colours of prey presented (50% for each colour) and one colour of stone in the background. This experiment suggests that the birds were selecting for crypsis by overlooking morphs that matched the stones in the background. This effect was even stronger when the background had a higher density of stones, probably because prey at the higher stone density are more likely to be hidden from the field vision of the bird so their density is effectively reduced or perhaps because the contrast of the unmatching prey is higher in this conditions. Another area of debate is that maybe some prey were masquerading as stones rather than being truly cryptic but there is no way of testing this with the existing data.

In experiment 3.2 the wild birds of Culiacán, Mexico selected against the morph that resembled the uncommon background elements. The most important conclusion of this experiment is that this selection was dependent on the background composition alone and not on the prey frequencies. These results lend support to the idea of parallelism originated by Endler (1978), because this kind of selection could result in a neutral equilibrium, with the frequencies of the morphs depending of the background composition. In other words selection would generate parallelism of morph frequency to background pattern element frequency and this parallelism could be either in time or space. This experiment results supports the findings of Giesel (1970, 1974), Owen (1966), Cook

(1983) and Cooper (1984) that visual predators generate parallelism of morph frequency and background composition when they select for crypsis.

In the experiments of Chapter IV (frequency-dependent experiments) evidence for crypsis was also found. Consistently in every experiment, when both prey were in a matching background, apostatic selection was stronger (Bond, 1983; Cooper, 1984b; Tucker and Allen, 1988) than when prey were presented in unmatching backgrounds. This suggests that crypsis also played a role in these experiments.

Experiment 5.1 (in Chapter V) provided yet more evidence for crypsis; it was not the main factor influencing selection but offered some protection to scattered prey among stones that match the background.

b) Apostatic Selection

“Parallelism of morph frequency and pattern element frequency is reinforced if there is frequency-dependent or apostatic selection by predators” (Endler, 1978). There is a lot of theoretical and some experimental evidence supporting the idea that apostatic selection can maintain polymorphism (Cain and Sheppard, 1954; Clarke, 1962; Allen and Clarke, 1968; Allen, 1973; Ayala and Campbell, 1974; Clarke 1979; Cooper, 1984b). Endler (1978) assumed that predators form search images to find cryptic prey. This condition needs to be met for the parallelism to occur. If predators simply select disproportionately the common prey polymorphism will be maintained but totally independently of the background composition. On the other hand if predators form search images then they will hunt on the basis of cues received from the common forms that distinguish them from the background. Such behaviour will be dependent of the background element composition and selection would stabilise the prey population at morph frequency equilibrium that will be entirely dependent on background colour element frequency (Cooper, 1984b). In other words, the majority of birds will learn to distinguish (form search images) the more cryptic prey because are more common, but at the same time a few birds will form search images of the rare form that is less cryptic (because it resembles less elements of the background). Therefore, the prey that resembles more elements of the background will continue to be the common form.

In my experiments (Chapter IV) apostatic selection was stronger when prey were in backgrounds that made them inconspicuous (the backgrounds used were natural grass and soil, and stones that matched the prey colours on hessian sheets). This implies the adoption of search images. Similar results were obtained in both Mexico and the UK. The obvious conclusion to this is that if that happens in nature then polymorphism would be maintained and the parallelism reinforced.

i. Stronger apostatic selection when prey matches the background

The results of experiments 4.2 and 4.3 showed that selection was apostatic in the experimental treatments (matching backgrounds) and also in the control experiments (unmatching backgrounds). The only, but important, difference was that during the experimental treatments apostatic selection was significantly stronger than in the control experiments treatments. Apostatic selection was probably stronger in the matching backgrounds because birds have to form stronger (or more detailed) search images for the common prey than in the case of unmatching backgrounds where prey have a higher contrast and search images are not required. Another possible factor interacting with frequency and crypsis is the density of the stones which also influenced selection in both cases matching and unmatching backgrounds. Apostatic selection increased as the density of stones increased and this was more dramatic in the matching backgrounds. The effect of stone density will be discussed in the next section.

c) The Effect of Background Complexity on Apostatic selection.

i. Prey density and the interaction with background interference

In theory, apostatic selection is more likely when prey density is low, because at high densities search images are not needed. Indeed selection may even be anti-apostatic (Allen and Clarke 1968, Allen 1972, Allen 1976, Cook and Miller 1977, Horsley et al. 1979, Allen and Anderson 1984). My experimental treatments with stones involved 50 prey (roughly 8.9 prey per square metre) which might be considered high density but the results in matching backgrounds tended to be apostatic and in some cases there was very strong selection against the common form. Selection was influenced by the density of the stones in the background. Proof of this was that in the treatment 'no stones' selection was anti-apostatic and when the stones were included in the background the strength of apostatic selection gradually increased (100, 200, 400, 600, 700, 1000 stones) (Chapter IV, experiment 4.2). A likely reason for this is that the presence of the stones means that fewer prey are visible to the birds and therefore the perceived density was effectively lower than it actually was. If birds have to search harder for prey then they are more likely to acquire search images for the common colour. Support for this idea of effective density is given by the presence of apostatic selection, albeit weaker, in experiments in non-matching backgrounds (Allen, *et al.* 1998; Weale, *et al.* 2000).

When I compared my results for 20 prey (3.5 per m²) in a background composed of 1000 matching stones against 50 prey (8.9 per m²) in 1000 matching stones the result was contradictory. Apostatic selection was stronger when the population consisted of 50 prey than 20 (Chapter IV, experiment

4.3). The possible explanation is that the stone 'interference' caused prey density (3.5 m² and 8.9 m²) to be perceived roughly as the same in both treatments, because with so many stones in the background is possible that many of the prey were hidden from view and therefore perceived as very low density in both cases. Backgrounds with 1000 stones at looked very complex to the human eye and any matching prey were difficult to detect.

It seems likely that prey densities in natural polymorphic cryptic prey are not a good guide because they appear to be very variable. Owen (1965) observed densities in the East African snail *Limicolaria martensiana* of up to 100 snails m² and the species *Thelsa pisana* at Zahara, in Andalusia, Spain has densities of 300 m² on clumps of vegetation (personal observations). *Cepaea nemoralis* occurs from 0.4 m² to 20 m² (Cain, *et al.* 1960). Work is needed to measure the effective density for a visually hunting bird. That way, a more realistic use of densities to test apostatic selection will be possible.

An important conclusion from my experiments is that 8.9 prey per square metre could be a realistic density for populations of real bait-sized prey and is also a good density for future experimentation testing apostatic selection.

d) Physical Protection

One point that Cooper (1984b) never talked about is the possibility that birds with their oblique view point could be failing to spot some of the prey that came to rest on the opposite side of a stone to where they were standing. He probably neglected this possibility because such anachoresis should, of course, be independent of frequency. However, it was undoubtedly a factor affecting risk of predation to any individual prey.

During the experiments of Chapter V the results of two experiments (5.2 and 5.3) did not follow the same pattern. In the experiment 5.2 grey prey resting close to a grey stone were more protected than brown prey resting close to brown stones, but results in experiment 5.3 every prey (matching or unmatching) was considerably more protected when close to stones. This might have happened because the conditions of the experiments were different. In the first experiment every prey was resting close to stones and, therefore birds in some cases form search images to find the unmatching prey. In the case of experiment 5.3 birds were simply concentrating on scattered prey that were easier to see or find and because only one prey colour was used, they may have encountered scattered matching prey first acquiring a search image and therefore easily found matching prey resting against stones. Clearly more work is needed to explore this finding.

(6.2) Predators

It's a well-known fact that wild birds participating during my experiments kill cryptic prey in nature. For example, *Quiscalus mexicanus* feeds on different worms, spiders, and grasshoppers and in some cases small river fish (personal observations). The Blackbird (*Turdus merula*) feeds on a wide range of prey like earthworms, caterpillars, snails, spiders, etc. (Collinge, 1941; Snow, 1958). In both cases some of the prey species are likely to be polymorphic for colour.

The behaviour of birds while feeding on pastry baits was probably no different from their natural behaviour (recordings by Lawrence (1984)) and this is supported by my own personal observations. The number of species of birds seen feeding during these experiments (8) and the number of individuals involved (around 250, Mexico and the UK) at several different sites is good evidence that ground-feeding birds have the potential to maintain polymorphism in real cryptic prey.

(6.3) Prey

One question that had been in my mind since I started these experiments concerns just how birds perceive the pastry baits between all the stones on the hessian sheet. Is crypsis influencing selection or is it masquerade or maybe anachoresis? Cooper (1984b) argued that masquerade is not possible because prey only resemble the stone in colour and not in shape. He (and I) never observed birds to peck at stones.

So how did birds perceive prey on the hessian–stones background? If they see the whole background as one big patch then it's safe to say that to be cryptic the prey should be a random sample of the background (Endler, 1984). On the other hand if they consider every stone as a small patch then the prey could be masquerading. This will be discussed in the next section. This question will remain unanswered until we have better understanding of bird perception of their surroundings.

(6.4) Background

The relationship of prey to patch size has important implications on how the relationship between the prey and the background is perceived by predators, and on how selection could promote polymorphism.

The problem of classifying patch size in relation to prey size is not only a function of the great diversity of background patch and cryptic prey sizes in nature; it also concerns the question of what

predators see as the indivisible unit of background colour patch. For example, consider an unbanded *Cepaea nemoralis* in its beechwood floor habitat (Greenwood, 1974). How is the background patchiness perceived by visual predators of *Cepaea*? In terms of individual dead brown beech leaves or in terms of the whole brown woodland floor?

Selection for crypsis within a large homogeneous colour patch will promote monomorphism (since there is only one way to be cryptic in the patch) and polymorphism in the population could only result from directional selection within the patches of different colours balanced by gene flow and migration between the big patches. Throughout my thesis where background patch size (stones) and prey size are similar (except in experiment 4.1) then selection cannot be realistically divided up into 'within' and 'between' patches but instead is best considered as acting within the multipatch background.

With the lack of information regarding patch size I only can suggest that the maintenance of polymorphism in cryptic prey purely by apostatic selection modified by crypsis is most likely to occur where prey size and background colour patch size are roughly the same (even when in the experiment 4.1 the patch size was bigger than prey and apostatic selection occurred). Increasing the patch size will introduce selection for matching microhabitat choice (Gillis, 1982), or selection will favour monomorphism within large patches (Endler, 1978).

(6.5) Recommendations for future work

Research never finishes and in this section I make suggestions on how my work could be extended.

(1) Try to test whether equilibrium is reached in an artificial prey population after simulating 25 generations (pioneered by Allen, 1973) to investigate whether background-tracing occurs and an equilibrium is reached depending on the frequency of matching elements in the background. In fact, Cooper (1984b) carried out such an experiment and I have recently extended this work in eight different sites (unpublished).

(2) More analysis is needed of data collected during the experiments published in this report. For example, the spectral data of stones and baits. After analysing these data the degree of similarity in colour between baits and stones can be established.

(3) Another important experiment would have the same design of experiment 4.2 in chapter IV where different frequencies of two colours of stones (grey and brown) in different densities were presented to birds, but this time using different stone colours and different bait colours, so we can

establish if this is a general response or just a particular response to brown and grey. Ideally, a number of different prey colour/background colour combinations would be used to test that the responses of the birds were a general phenomena associated with the matching of any colour with components of a background, not just grey and brown.

(4) The question of the density dependence of apostatic selection is still largely unresolved. Experiments at very low densities using the Copper's design of stones and baits would create practical problems but experiments at some representative densities from natural prey should be possible and extremely useful.

(5) Field investigations seem an obvious direction for further research on apostatic selection on cryptic prey in order to test whether wild predators select in apostatic fashion when hunting for cryptic polymorphic prey. Now that colour video equipment is portable and easy to use, quality recordings of birds feeding on their natural prey could be made for later detailed analysis. There appear to be two main options: wild predators could be observed feeding on their natural undisturbed prey populations or they could be observed feeding on natural prey in which the morph frequencies have been altered.

(6.6) Final Remarks

An important conclusion from this work is that similar selective behaviour of birds was observed in both the UK and Mexico. The experiments involved very different species in very different habitats. In both countries birds selected against the unmatching prey and against the common form (apostatic selection) in an almost identical way. This is very important because we can now say that apostatic selection is likely to be a general behavioural trend in ground-feeding birds and could therefore play a very significant role in the maintaining of cryptic polymorphic prey in nature.

In general, previous studies (Allen, 1973; Bond, 1983; Cooper, 1984b; Weale, *et al.* 2000) have focused their experimental designs in prey frequencies and prey densities presented at just one level of complexity in the background. This work for the first time, explored the effect of the background complexity and the position of prey in selection by wild birds.

Appendix

Table 1 Pair wise comparisons of the different regression slopes (b values) of β on frequency for experiment 4.2, with the Bonferroni method for Multiple Comparisons.

Treatments		Mean Difference	Standard Error	P	95% confidence interval for difference	
1 st treatment of pair	2 nd treatment of pair				Lower bound	Upper bound
1 (no stones slope)	2	-20.556	2.568	.016	-37.200	-3.912
	3	-19.269	3.273	NS	-40.485	1.947
	4	-57.909	6.264	.007	-98.506	-17.313
	5	-40.135	5.445	.025	-75.427	-4.842
	6	-42.393	2.201	.001	-56.656	-28.130
	7	-32.689	2.971	.003	-51.942	-13.436
	8	-99.426	10.097	.005	-164.870	-33.982
	9	-52.230	4.228	.001	-79.630	-24.830
	10	-105.740	4.717	.001	-136.311	-75.169
	11	-44.422	3.433	.001	-66.673	-22.172
	12	-130.411	3.960	.001	-156.076	-104.746
	13	-53.155	3.149	.001	-73.562	-32.748
	2 (100 matching stones slope)	1	20.556	2.568	.016	3.912
3		1.287	2.862	NS	-17.259	19.834
4		-37.353	5.201	.029	-71.063	-3.642
5		-19.579	5.999	NS	-58.462	19.305
6		-21.837	3.134	.034	-42.151	-1.523
7		-12.133	2.436	NS	-27.922	3.656
8		-78.870	11.370	.035	-152.562	-5.177
9		-31.674	5.769	NS	-69.064	5.716
10		-85.184	4.874	.001	-116.775	-53.593
11		-23.866	4.622	NS	-53.820	6.088
12		-109.855	3.781	.001	-134.363	-85.346
13		-32.598	4.048	.015	-58.833	-6.364
3 (100 unmatching stones slope)		1	19.269	3.273	NS	-1.947
	2	-1.287	2.862	NS	-19.834	17.259
	4	-38.640	5.767	.042	-76.021	-1.260
	5	-20.866	6.970	NS	-66.040	24.308
	6	-23.124	2.253	.004	-37.729	-8.518
	7	-13.420	2.710	NS	-30.982	4.142
	8	-80.157	12.588	.055	-161.740	1.427
	9	-32.961	6.567	NS	-75.521	9.598

	10	-86.471	2.781	.001	-104.495	-68.447
	11	-25.153	4.809	NS	-56.324	6.017
	12	-111.142	4.557	.001	-140.677	-81.607
	13	-33.886	3.859	.009	-58.899	-8.872
4 (200	1	57.909	6.264	.007	17.313	98.506
matching	2	37.353	5.201	.029	3.642	71.063
stones	3	38.640	5.767	.042	1.260	76.021
slope)	5	17.774	7.625	NS	-31.648	67.196
	6	15.516	5.189	NS	-18.118	49.151
	7	25.220	5.236	NS	-8.716	59.156
	8	-41.517	11.000	NS	-112.809	29.775
	9	5.679	8.249	NS	-47.782	59.140
	10	-47.831	7.258	.046	-94.869	-.792
	11	13.487	7.896	NS	-37.691	64.665
	12	-72.502	4.884	.001	-104.157	-40.846
	13	4.755	6.683	NS	-38.558	48.067
5 (200	1	40.135	5.445	.025	4.842	75.427
unmatching	2	19.579	5.999	NS	-19.305	58.462
stones	3	20.866	6.970	NS	-24.308	66.040
slope)	4	-17.774	7.625	NS	-67.196	31.648
	6	-2.258	6.436	NS	-43.974	39.458
	7	7.446	4.914	NS	-24.404	39.296
	8	-59.291	8.958	.045	-117.348	-1.234
	9	-12.095	5.984	NS	-50.880	26.690
	10	-65.605	7.559	.010	-114.600	-16.610
	11	-4.287	3.999	NS	-30.207	21.633
	12	-90.276	5.140	.001	-123.591	-56.961
	13	-13.020	3.952	NS	-38.631	12.591
6 (400	1	42.393	2.201	.001	28.130	56.656
matching	2	21.837	3.134	.034	1.523	42.151
stones	3	23.124	2.253	.004	8.518	37.729
slope)	4	-15.516	5.189	NS	-49.151	18.118
	5	2.258	6.436	NS	-39.458	43.974
	7	9.704	2.902	NS	-9.108	28.515
	8	-57.033	10.702	NS	-126.395	12.329
	9	-9.837	5.310	NS	-44.255	24.581
	10	-63.347	3.818	.001	-88.093	-38.601
	11	-2.029	4.494	NS	-31.159	27.101
	12	-88.018	4.138	.001	-114.837	-61.199
	13	-10.762	3.505	NS	-33.478	11.955

7 (400	1	32.689	2.971	.003	13.436	51.942
unmatching	2	12.133	2.436	NS	-3.656	27.922
stones	3	13.420	2.710	NS	-4.142	30.982
slope)	4	-25.220	5.236	NS	-59.156	8.716
	5	-7.446	4.914	NS	-39.296	24.404
	6	-9.704	2.902	NS	-28.515	9.108
	8	-66.737	10.711	.062	-136.157	2.683
	9	-19.541	5.654	NS	-56.185	17.103
	10	-73.051	4.076	.001	-99.470	-46.631
	11	-11.733	3.584	NS	-34.963	11.496
	12	-97.722	4.271	.001	-125.402	-70.042
	13	-20.466	2.177	.006	-34.577	-6.355
8 (600	1	99.426	10.097	.005	33.982	164.870
matching	2	78.870	11.370	.035	5.177	152.562
stones	3	80.157	12.588	.055	-1.427	161.740
slope)	4	41.517	11.000	NS	-29.775	112.809
	5	59.291	8.958	.045	1.234	117.348
	6	57.033	10.702	NS	-12.329	126.395
	7	66.737	10.711	.062	-2.683	136.157
	9	47.196	9.127	NS	-11.958	106.350
	10	-6.314	13.091	NS	-91.163	78.535
	11	55.003	10.396	NS	-12.375	122.382
	12	-30.985	11.153	NS	-103.272	41.302
	13	46.271	10.039	NS	-18.793	111.335
9 (600	1	52.230	4.228	.001	24.830	79.630
unmatching	2	31.674	5.769	NS	-5.716	69.064
stones	3	32.961	6.567	NS	-9.598	75.521
slope)	4	-5.679	8.249	NS	-59.140	47.782
	5	12.095	5.984	NS	-26.690	50.880
	6	9.837	5.310	NS	-24.581	44.255
	7	19.541	5.654	NS	-17.103	56.185
	8	-47.196	9.127	NS	-106.350	11.958
	10	-53.510	8.337	.053	-107.546	.526
	11	7.808	3.649	NS	-15.844	31.460
	12	-78.181	5.489	.001	-113.758	-42.604
	13	-.925	4.704	NS	-31.410	29.561
10 (700	1	105.740	4.717	.001	75.169	136.311
matching	2	85.184	4.874	.001	53.593	116.775
stones	3	86.471	2.781	.001	68.447	104.495
slope)	4	47.831	7.258	.046	.792	94.869

	5	65.605	7.559	.010	16.610	114.600
	6	63.347	3.818	.001	38.601	88.093
	7	73.051	4.076	.001	46.631	99.470
	8	6.314	13.091	NS	-78.535	91.163
	9	53.510	8.337	.053	-.526	107.546
	11	61.318	5.952	.004	22.743	99.893
	12	-24.671	6.446	NS	-66.449	17.107
	13	52.585	4.667	.002	22.337	82.834
11 (700	1	44.422	3.433	.001	22.172	66.673
unmatching	2	23.866	4.622	NS	-6.088	53.820
stones	3	25.153	4.809	NS	-6.017	56.324
slope)	4	-13.487	7.896	NS	-64.665	37.691
	5	4.287	3.999	NS	-21.633	30.207
	6	2.029	4.494	NS	-27.101	31.159
	7	11.733	3.584	NS	-11.496	34.963
	8	-55.003	10.396	NS	-122.382	12.375
	9	-7.808	3.649	NS	-31.460	15.844
	10	-61.318	5.952	.004	-99.893	-22.743
	12	-85.989	4.791	.001	-117.042	-54.936
	13	-8.732	1.968	NS	-21.491	4.026
12 (1000	1	130.411	3.960	.001	104.746	156.076
matching	2	109.855	3.781	.001	85.346	134.363
stones	3	111.142	4.557	.001	81.607	140.677
slope)	4	72.502	4.884	.001	40.846	104.157
	5	90.276	5.140	.001	56.961	123.591
	6	88.018	4.138	.001	61.199	114.837
	7	97.722	4.271	.001	40.042	125.402
	8	30.985	11.153	NS	-41.302	103.272
	9	78.181	5.489	.001	42.604	113.758
	10	24.671	6.446	NS	-17.107	66.449
	11	85.989	4.791	.001	54.936	117.042
	13	77.256	4.707	.001	46.750	107.763
13 (1000	1	53.155	3.149	.001	32.748	73.562
unmatching	2	32.598	4.048	.015	6.364	58.833
stones	3	33.886	3.859	.009	8.872	58.899
slope)	4	-4.755	6.683	NS	-48.067	38.558
	5	13.020	3.952	NS	-12.591	38.631
	6	10.762	3.505	NS	-11.955	33.478
	7	20.466	2.177	.006	6.355	34.577
	8	-46.271	10.039	NS	-111.335	18.793

9	.925	4.704	NS	-29.561	31.410
10	-52.585	4.667	.001	-82.834	-22.337
11	8.732	1.968	NS	-4.026	21.491
12	-77.256	4.707	.001	-107.763	-46.750

*Based on estimated marginal means.

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