

Frequency-Dependent Selection by Predators [and Discussion]

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Frequency-dependent selection by predators

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Sometimes predators tend to concentrate on common varieties of prey and overlook rare ones. Within prey species, this could result in the fitness of each variety being inversely related to its frequency in the population. Such frequency-dependent or ‘apostatic’ selection by predators hunting by sight could maintain polymorphism for colour pattern, and much of the supporting evidence for this idea has come from work on birds and artificial prey. These and other studies have shown that the strength of the observed selection is affected by prey density, palatability, coloration and conspicuousness. When the prey density is very high, selection becomes ‘anti-apostatic’: predators preferentially remove rare prey. There is still much to be learned about frequency-dependent selection by predators on artificial prey: work on natural polymorphic prey has hardly begun.

INTRODUCTION

Although most predators exist on a varied diet, they rarely eat the different types of prey in proportions equivalent to their relative abundance in the environment. Sometimes relative prey abundance has a direct effect on choice, so that predators tend to concentrate on a prey type when it is common and overlook it when it is rare, or conversely, concentrate on rare prey and ignore common ones. This flexibility of prey choice with availability can cause the fitness of a prey type to be a function of frequency, negative in the first case and positive in the second. The selection is thus frequency dependent (Ayala & Campbell 1974), and has the potential for increasing or decreasing genetic diversity within populations and species diversity within communities (Clarke 1962*a*; Murdoch 1969).

Much of the impetus for the development of ideas on frequency-dependent selection by predators has been inspired by the widespread phenomenon of balanced colour polymorphism, the simultaneous occurrence in the same population of two or more inherited phenotypes with discrete colour patterns. A satisfactory explanation for the persistence of colour polymorphism has long been sought. Poulton (1884) hinted that the brown–green dimorphism in the larvae of geometrid moths (*Cyclophora* spp.) could be maintained by predators that concentrate on the commoner morph and neglect the rarer one (Allen & Clarke 1984). Seventy years later this mechanism was mentioned briefly as a possible explanation for the maintenance of the complex shell pigment polymorphisms of landsnails such as *Cepaea* (Cain & Sheppard 1954; Haldane 1955). The case was argued forcefully by Clarke (1962*a*), who supported the hypothesis with data drawn not only from his own field surveys of *Cepaea* (Clarke 1962*b*) but also from the limited number of relevant predator–prey studies that were then available (see, for example, Popham 1941, 1942; De Ruiter 1952; Reighard 1908; Tinbergen 1960). Moment (1962) independently reached similar conclusions about the maintenance of massive polymorphism in marine organisms such as brittlestars (*Ophiopholis aculeata*) and butterfly clams (*Donax variabilis*).

The literature on frequency-dependent prey selection has evolved from the disparate

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disciplines of genetics, ecology, animal behaviour and psychology and it is not surprising that the terminology is correspondingly at odds. There are at least four different terms for the tendency of predators to take an excess of prey when common and a deficit when rare: 'apostatic selection' (Clarke 1962*a*), 'reflexive selection' (Moment 1962; Owen & Whiteley 1986), 'switching' (Murdoch 1969) and 'matching selection' (Bond 1983). Strictly, the first two refer to the effect of predator choice on the prey population whereas the last two describe the choice itself. Greenwood (1984, 1985), in drawing attention to the semantic difficulties of distinguishing between negative and positive frequency-dependent selective predation, has suggested that two types of apostatic selection should be recognized: 'pro-apostatic' and 'anti-apostatic' (also called 'unifying selection' (Pielowski 1959, 1961) and 'oddity selection' (Bond 1983)). In this paper I use the terms 'apostatic selection' in the original sense of selection that acts against common forms and 'anti-apostatic selection' in the sense of selection against rare forms.

Of the two, apostatic selection perhaps has the more interesting evolutionary implications, because it can lead to a stable equilibrium of morph frequency and so contribute to the maintenance of the enormous genetic diversity present in natural populations (Clarke 1979). It will therefore be the focus of most of my remarks. I intend to explore the extent to which apostatic selection has been tested experimentally and I shall concentrate on those experiments in which the prey were, or were meant to represent, different genetic morphs of the same species. I feel justified in omitting a full discussion of the 'switching' literature (see Murdoch & Oaten (1975), Lawton *et al.* (1974) and Greenwood & Elton (1979) for reviews), because much of this is concerned with prey that are different species and differ in their anatomy, behaviour and ecology much more than do morphs within a population of a single species. The mechanisms that lead to switching between prey species are therefore likely to be rather different from those that lead to switching between morphs. I shall not consider morphs that are Batesian mimics of other, more noxious, potential prey.

CAUSES OF APOSTATIC SELECTION

The designs of early experiments to test apostatic selection were greatly influenced by the ideas of Tinbergen (1960). He had shown that tits (*Parus* spp.) concentrated their efforts on palatable, cryptic, prey species that were abundant, and tended to ignore those that were at low and very high densities. He concluded that the birds acquire 'search images' through chance encounters with prey; in other words, that they learn those cues that enable them to distinguish the prey from the background. He claimed that search images are unlikely to be formed when the prey are scarce (because the rate of encounter would be too low for learning to occur) and are likely to be undetectable at very high densities (perhaps because the birds would favour a mixed diet). Within these limits, the more abundant the prey, the quicker search images would be formed and the more likely the prey would be exploited.

Clarke (1962*a*, 1969) transferred the idea of search image to predation acting on variation within species, pointing out that a tendency to form search images for common morphs rather than rare ones could be the proximate cause of frequency-dependent selection (and the consequent maintenance of the polymorphism). He went on to predict that any factor that decreases the encounter rate with the prey should lessen the chances of search image formation and, by extrapolation, apostatic selection and the degree of polymorphism.

We now realize that the presence of apostatic selection does not necessarily imply that the predators are hunting by search images (Krebs 1973; Greenwood 1984; Allen 1984). In fact, search images are unlikely to be involved when the prey are conspicuous (a property that Clarke (1962*a*) attributed to some morphs of *Cepaea*) because the strict definition of search image is 'a perceptual change in the ability of predators to detect *cryptic* prey' (Tinbergen 1960; Dawkins 1971; Krebs 1973; Lawrence & Allen 1983; but see Endler, this symposium, for an alternative view). In addition, the very existence of search images has been questioned. Tinbergen's explanation was criticized by Royama (1970) on the grounds that the birds could have been learning to exploit profitable patches, a possibility that has gained experimental support (for example by Smith & Sweatman (1973)). More recently, Guilford & Dawkins (1987) have gone so far as to suggest that there is no convincing support for search images from any of the published studies (Dawkins 1971; Pietrewicz & Kamil 1979, 1981; Gendron 1986; Lawrence 1985*a, b*, 1986) and claim that all the apparent evidence can be explained by predators simply slowing down their rate of search.

Apostatic selection will result from any proximate mechanism that causes the risk to a prey type to increase disproportionately with increasing frequency. Although an array of such mechanisms have been listed by Murdoch *et al.* (1975) and Greenwood (1984), many of these are not applicable to morphs within species, because they depend on prey types differing in properties other than coloration, such as their distribution in space, the techniques needed to capture them, the techniques needed to handle them, and so on (for recent examples, see Bergelson (1985) and Corthran & Thorp (1985)).

The ultimate cause of apostatic selection could be that by concentrating on common morphs predators maximize net energy consumption (and therefore fitness). Evidence that this is the case (for cryptic prey) is implied by Croze's (1970) observation that the rate of predation by carrion crows (*Corvus corone*) was higher when they were exploiting each of three monomorphic populations of painted mussel shells than when they were feeding on a trimorphic population with equal numbers of the three types. More recently, evidence has been obtained that humans do indeed 'feed' most rapidly when they concentrate on the common morph in a 'population' of four computer-generated 'morphs' on the screen of a colour monitor (Weale *et al.* 1988). However, the interpretation of apostatic selection in terms of optimal foraging theory is undoubtedly difficult when the 'prey' are painted sea-shells or pixels on a monitor, because we do not know how colour affects the predator's estimate of profitability, or net reward per unit handling time (Hubbard *et al.* 1982).

DEMONSTRATING APOSTATIC SELECTION

In our first investigation (Allen & Clarke 1968) we used wild passerine birds and green and brown cylindrical 'baits' (made from lard, flour and colouring, after Turner (1961)). A previous unsuccessful attempt to test apostatic selection with songthrushes (*Turdus philomelos*) and *Cepaea hortensis* in two small aviaries had convinced us of the value of using free-ranging predators in their normal surroundings (Clarke 1961). Despite the obvious criticisms, artificial prey have the advantage of being easy to standardize and easy to make in quantity. The experiment was tackled from the standpoint of population genetics rather than animal behaviour: we looked for selection exerted by birds feeding *en masse* on large 'populations' of baits. The birds we used were those that feed in most British suburban gardens; for example,

the blackbird (*Turdus merula*), songthrush (*T. philomelos*), starling (*Sturnus vulgaris*), dunnock (*Prunella modularis*) and house sparrow (*Passer domesticus*).

Trained wild birds

In one approach (Allen & Clarke 1968), wild birds were fed on one colour alone for several days, given a 'population' of equal numbers of brown and green at a density of 2 m^{-2} , trained on the second colour, and again presented with an equal choice. The '1:1' ratios were kept constant by frequent replacement of eaten prey. After each session of training there was a strong 'training bias' (Curio 1976), or tendency for the birds to remove an excess of the familiar colour. A further 12 experiments confirmed this effect (Allen 1974). We assumed that the birds acquired search images for the familiar colours but this explanation now seems unlikely, given that the two prey types appeared conspicuous (at least to the human eye) on the grass background (Krebs 1973; Dawkins 1971; Lawrence & Allen 1983). A more likely explanation is that, in common with many other predators, birds simply prefer familiar food (Partridge 1981). Leaving aside the exact nature of the underlying behaviour, the implications were that if, through chance, a predator encounters and eats a succession of identical prey then it would be likely to overlook subsequent prey items that are different. This could happen when a predator feeds on a polymorphic population with one morph much more common than the rest. A '1:1' population in a training experiment can be regarded as one in which one of the colours, the familiar one, is far more abundant than the other.

Training experiments have been criticized on the grounds that they are too unnatural (Cain 1983) and that they do not necessarily provide evidence for apostatic selection, because an increase in familiarity with a common prey is not the only behaviour that could be a proximate cause of frequency-dependent selection (Greenwood & Elton 1979; Greenwood 1985). It might be, for example, that predators sample the prey, estimate which form is the commonest and switch to it because they have an innate preference for prey that are common (Krebs 1973). In defence of training experiments they at least test one of the possible mechanisms responsible for apostatic selection (in the same way that any experiment designed to test apostatic selection tests only one of the possible mechanisms that could be responsible for maintaining variation).

Naïve wild birds

Our second approach (Allen & Clarke 1968) was to offer, to 'untrained' birds, populations with one colour nine times as common as the other, again at a density of 2 m^{-2} . This design invoked fewer assumptions about the behavioural basis of apostatic selection. A population with green as the common colour was presented for a number of days and then changed for one with green rare (to control for possible frequency-independent selection caused, for example, by innate or learned colour preferences outside the experiment). Eaten prey were replaced frequently to keep the proportions close to the original 9:1 ratio. The populations were watched continuously and separate data were recorded for four groups of species (blackbirds and songthrushes, starlings, dunnocks, house sparrows). When the grand totals for the two parts of the experiment were compared, all species groups appeared to select in a manner predicted from the hypothesis of apostatic selection. Although all the groups had strong colour preferences irrespective of frequency (for example, blackbirds and songthrushes had a frequency-independent preference for brown), overall the preference for a given colour was stronger when that colour was common. This first experiment was not conclusive, however,

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because the grand totals masked considerable heterogeneity within the data; for example, among days for house sparrows, and among visits for blackbirds and songthrushes. Confirmation that the selection overall tends to be apostatic was provided by the results from replicates involving seventeen groups of birds at ten other sites: in all seventeen the preference for a given colour was stronger when that colour was common (Allen 1973, 1976).

It is important to note that the strong frequency-independent selection against brown would probably lead to its elimination, were the two colours morphs of a real species (although experiments at very extreme frequencies would be needed to check whether this is so). The observed change in the selection against brown is thus probably only 'potentially apostatic' (Greenwood 1985). The resulting selection would be apostatic in effect if the brown morph were at a disadvantage in some other respect: for example, in its physiology.

TABLE 1. INVESTIGATING APOSTATIC SELECTION ON ARTIFICIAL, SEMI-NATURAL AND REAL POLYMORPHIC PREY: TRAINING EXPERIMENTS

(The number of prey refers to the number of 'morphs' in the 'population'. f, Field; l, laboratory; t.b., training bias.)

reference	predators	prey	place	result	comments
(a) prey artificial					
Allen & Clarke (1968)	wild birds	baits (2: green, brown)	f	t.b.	t.b. unaffected by background?
Allen (1974)					
Allen (1973)					
Allen (1984)	wild birds	baits (9: various hues of green and brown in a quasi-continuous distribution)	f	t.b.	training on modal colour resulted in increased variance of prey population
Croze (1970)	crows (<i>Corvus corone</i>)	mussel shells over meat (2: various combinations of shapes and colours)	f	t.b.	prey cryptic; t.b. affected by degree of similarity of prey
Oates (in Cook 1971)	wild birds	baits (red, yellow)	f	t.b.	
Raymond (1984, 1987)	wild birds	flat baits (2: striped, plain)	f	t.b.	prey ground colour cryptic
Shelton (1986)	wild birds	baits (2: discoid, cylindrical)	f	t.b.	t.b. caused by visual preference or familiarity with handling technique?
Soane & Clarke (1973)	laboratory mice	baits (2: peppermint, vanilla)	l	t.b.	t.b. for familiar scent
(b) prey natural or semi-natural intraspecific variants					
Allen <i>et al.</i> (1988)	wild birds	<i>Cepaea hortensis</i> (2: Y0, Y5)	f	t.b.	shells filled with pastry
Clarke (1961)	songthrushes (<i>Turdus philomelos</i>)	<i>Cepaea hortensis</i> (2: Y0, Y5)	l	no t.b.	no consistent selection; birds too familiar with aviary?
den Boer (1971)	coal tit (<i>Parus ater</i>)	moth larvae (<i>Bupalus piniarius</i>) (2: green, yellow)	l	t.b.?	only one bird; green cryptic, yellow conspicuous; trained on green only
Harvey <i>et al.</i> (1975)	songthrushes	<i>Cepaea nemoralis</i> & <i>C. hortensis</i> (2: Y0, B0)	f	t.b.	shells filled with breadcrumbs; t.b. for colour stronger than t.b. for size?

TABLE 2. INVESTIGATING APOSTATIC SELECTION ON ARTIFICIAL, SEMI-NATURAL AND REAL POLYMORPHIC PREY:

MULTI-FREQUENCY EXPERIMENTS

(a.s., apostatic selection; pot. a.s., potential apostatic selection; f.d.s., frequency-dependent selection. For remaining abbreviations, see table 1.)

reference	predators	prey	place	result	comments
(a) prey artificial					
Allen & Clarke (1968)	wild birds	baits (2: green, brown)	f	pot. a.s.	a.s. unaffected by background?
Allen (1972, 1976)	domestic pigeons	'seeds' (2: beans, wheat)	l	a.s.	a.s. stronger when prey inconspicuous
Bond (1983)	(<i>Columba livia</i>)				
Cook & Miller (1977)	Japanese quail	baits (2: blue, red)	l	a.s.	a.s. increased with density
	(<i>Coturnix coturnix</i>)				
Cooper (1984a, b)	wild birds	baits (2: orange, grey)	f	a.s.	a.s. stronger when prey inconspicuous
Fullick & Greenwood (1979)	domestic chicks	crumbs (2: green, brown)	l	a.s.	
Gendron (1982)	bobwhite quail	baits (2: green, brown)	l	a.s.	a.s. when prey inconspicuous; no a.s. when conspicuous?
	(<i>Coturnix virginianus</i>)				
Greenwood <i>et al.</i> (1981)	wild birds	baits (2: yellow, red)	f	no f.d.s.	both morphs unpalatable
Greenwood <i>et al.</i> (1981)	domestic chicks	chick crumbs (2: green, brown)	l	a.s.	a.s. weaker when both prey unpalatable than when both palatable
Harvey <i>et al.</i> (1974)	wild birds	baits (2: green, brown)	f	a.s.	very high prey density; only 2 expts
Horsley (1978)	wild birds	baits (2: yellow, brown)	f	no f.d.s.	no evidence for effect of either frequency or density
Manly <i>et al.</i> (1972)	Japanese quail	baits (2: blue, red)	l	a.s.	first expt with a wide range of frequencies
Shelton (1986)	wild birds	baits (2: discoid, cylindrical)	f	a.s.	
Shelton (1986)	wild birds	baits (11: various shapes, in quasi-continuous distribution)	f	a.s.	selection against modal colour increased variance of prey population
Tucker & Allen (1988)	humans	computer-generated images (2: T-shape, circle)	l	a.s.	a.s. when inconspicuous, not when conspicuous
Weale <i>et al.</i> (1988)	humans	computer-generated images (4: different shapes)	l	a.s.	a.s. by adults, not by children
Willis <i>et al.</i> (1980)	domestic chicks	crumbs (2: red, green; green, yellow; red, yellow)	l	no f.d.s.	
Willis <i>et al.</i> (1980)	domestic chicks	crumbs (2: green, brown)	l	irregular a.s.	no effect of density
(b) prey natural or semi-natural intraspecific variants					
R. W. Arnold (unpublished)	songthrushes	<i>Cepaea nemoralis</i> (2: P0, Y0; B0, Y0)	f	a.s.?	an attempt to test a.s. in artificial colonies of live <i>Cepaea</i>
Maskell <i>et al.</i> (1977)	sticklebacks	<i>Astellus aquaticus</i> (2: light, dark)	l	a.s.	'morphs' were extreme phenotypes from a continuous distribution
	(<i>Gasterosteus aculeatus</i>)				
Popham (1941, 1942)	Rudd (<i>Scardinius erythrophthalmus</i>)	<i>Sigara distincta</i> (3: different shades of brown)	l	a.s.	'morphs' environmentally determined; data reanalysed by Clarke (1962a)
Reid (1987)	unknown	<i>Littoraria filosa</i> (2: yellow, brown)	f	a.s.	manipulation of morph frequencies on mangroves
G. M. Tucker (unpublished)	songthrushes	<i>Cepaea hortensis</i> (2: Y5, Y0)	l	a.s.?	four birds tested

Other demonstrations

Evidence for apostatic selection on artificial and natural morphs has now been demonstrated in a variety of predators and prey. The experiments fall into two main categories: those that involve training (table 1) and those that do not (table 2).

For practical reasons, most ecological geneticists have tested apostatic selection with totally artificial 'prey' differing, so far as they know, in colour alone. A few studies have used natural intra-population variants, and in most of these there was an element of artificiality: for example, empty *Cepaea* shells stuffed with bread (Harvey *et al.* 1975) or with pastry (Allen *et al.* 1988). Very little of the work listed in tables 1 and 2 used real live morphs.

Birds, undoubtedly significant predators of terrestrial prey (including many polymorphic species), have featured prominently. Much less attention has been paid to other groups that also hunt by sight, have colour vision, and are therefore potentially capable of maintaining colour polymorphisms (tables 1 and 2). There has been some work on testing apostatic selection by small mammals that use olfactory cues (Soane & Clarke 1973; Greenwood *et al.* 1984*a, b*).

Measuring frequency-dependent selection

Considerable progress has been made in the development of statistical methods for the detection and measurement of apostatic selection, especially for ideal experiments in which a range of frequencies are presented. Experiments of this sort can now be designed more effectively. At least two analytical methods can be used to estimate the strengths of the frequency-dependent and frequency-independent components of the observed selection in a given experiment, and the relative merits of the methods have been discussed extensively by Elton & Greenwood (1970), Greenwood & Elton (1979), Manly (1973, 1974, 1985) and Gendron (1987). Partly as a result of these improvements in analysis, we now have a better idea of the factors that affect the magnitude of apostatic selection. But, as I hope to make clear, there are still many gaps in our knowledge.

FACTORS AFFECTING THE STRENGTH OF APOSTATIC SELECTION

Clarke (1962*a*) predicted that the magnitude of apostatic selection acting on a polymorphic population would be affected by the palatability, density and conspicuousness of the prey. He also predicted that its strength would be related to the degree of difference in coloration of the morphs and the number of morphs in the population.

Morph coloration and distinctness

Whatever the proximate cause of a preference for a common morph, it seems reasonable to assume (for palatable prey) that a rare morph which is similar in appearance to the common morph is more likely to be attacked than one that is different. Nearly all the experiments listed in tables 1 and 2 used prey that were very different indeed in appearance. Although some morphs in some species are as different as, say, our green and brown baits, there are plenty of examples where they are very similar: the various shades of yellow in *Cepaea*, for example. In fact, wild birds trained to search for buff (made from equal parts of green and brown pastry) will continue to take this colour in preference to baits made from, say, six parts green and two

parts brown, or even five parts green and three parts brown (Allen 1984). Similarly, six training experiments by Raymond (1984) showed that birds preferred the familiar of green prey that differed in the presence or absence of a single narrow red stripe. The same effect was obtained when the prey were even more similar: plain green and green with a single green stripe (Raymond 1987). Because of the lack of control of the degree of training for the individual birds these experiments were too crude to measure the preferences accurately. Nevertheless, the training effects detected by Allen (1984) and Raymond (1984, 1987) do seem to be less than those in the comparable experiments with the more contrasting colours of green and brown (Allen 1974). By the same token, crows selectively detected cryptic shells of the familiar colour when given a choice and the chances of them detecting other shells depended on the degree of resemblance to the familiar shell (Croze 1970). These various experiments with similar prey thus support the prediction that one effect of apostatic selection is to increase the differences in morph coloration (Clarke 1962*a*); that is, their degree of disassociation (Murray 1972) or diversity of 'aspect' (Rand 1967).

In nature, the morphs of many species are adorned with patterns (stripes, blotches, flammules, etc.) in colours that contrast with the ground pigment. Work on such patterned prey is in its infancy; nearly all the experiments listed in tables 1 and 2 used plain prey. The training experiments carried out by Raymond (1984, 1987), mentioned above, are an exception. It is encouraging to the hypothesis of apostatic selection that comparable results were obtained by Allen *et al.* (1988) using yellow unbanded and yellow five-banded morphs of *Cepaea hortensis*, albeit empty shells stuffed with pastry (following the method of Harvey *et al.* (1975)). We designed these experiments to the recommendations of Bantock & Harvey (1974) in that an additional 1:1 population was presented at the start of the experiment. We did six experiments with wild birds. Selection after nine of the twelve sessions of training was in the direction predicted from the hypothesis that birds prefer familiar morphs.

Not only have most of the prey differed in colour alone but there has also been a bias towards the use of plain green and plain brown (tables 1 and 2). Brown and green morphs occur in some terrestrial polymorphic species (Owen 1980), but we require work on more colours to confirm that apostatic selection is a general property of predators that hunt by sight.

Number of morphs

All the experiments listed in tables 1, 2 and 3 used dimorphic populations, apart from those of Popham (1941, 1942) and Weale *et al.* (1988). Clarke (1962*a*) reanalysed Popham's data on selective predation by rudd (*Scardinius erythrophthalmus*) on three colour varieties of corixid water bugs (*Sigara distincta*) and made the interesting suggestion that once an apostatic polymorphism becomes established the more readily it would "take in" varieties which in a monomorphic population would be eliminated'. The greater the degree of polymorphism, the stronger the apostatic selection, and vice versa. The experiments by Weale *et al.* showed that human subjects do exert apostatic selection when searching in a 'population' of four cryptic 'morphs' on a colour monitor but a comparable experiment with a smaller number of morphs was not done.

Palatability

We should not expect predators to maintain polymorphisms in species which are common and highly palatable, because rare morphs would be encountered often enough for predators to learn that they are profitable (Clarke 1962*a*). Why then has apostatic selection been

demonstrated so often in artificial prey? One possible answer is that, relative to alternative food, artificial prey are only of moderate acceptability. In my own experiments, individual birds would often be absent from the bait populations for hours, and when they did visit they would frequently ignore the baits and hunt for earthworms (J. A. Allen, unpublished observations).

We should also not expect predators to maintain polymorphisms in unpalatable species (Clarke 1962*a*). Conventional ideas about the evolution of warning coloration assume that rare variants in a population would be at a selective disadvantage compared with common forms because predators would be less likely to remember their noxious qualities. Selection is therefore expected to be anti-apostatic and would thus decrease diversity. In fact, the evidence available from two experiments fails to support this view (Greenwood *et al.* 1981). Frequency-dependent selection was absent in an experiment with wild birds and yellow and red pastry baits made distasteful by the addition of quinine sulphate. In the second experiment, with domestic chicks and distasteful green and brown chick crumbs, frequency-dependent selection was detected but, unexpectedly, it was apostatic (although weaker than in a similar experiment with palatable green and brown crumbs). Greenwood *et al.* (1981) suggest that hungry individuals may select apostatically, whereas satiated individuals may select anti-apostatically; the proportion of the two will determine whether selection overall is apostatic, anti-apostatic, or neither. Apostatic selection could therefore provide the explanation to the apparent paradox that many aposematic species are polymorphic (see Edmunds (1974) for examples). Recently, the more conventional view has been upheld: anti-apostatic selection has been demonstrated in a carefully controlled experiment with wild birds and pastry baits (Greenwood *et al.* 1988).

Conspicuousness

It had been argued that apostatic selection would be strongest when the morphs are conspicuous in coloration (Clarke 1962*a*) and therefore we made no attempt in the early experiments to match the prey to the colour and structure of the background. (Of course, as discussed above, it is now clear that the idea that morphs are conspicuous is contradictory to the idea that apostatic selection is caused by search images.) To our eyes, the 'standard' brown and green baits were conspicuous against the substratum, whether grass lawn or bare soil (Allen & Clarke 1968; Allen 1976), and the same applies to most of the other prey listed in tables 1 and 2, apart from those used by Bond (1983), Cooper (1984*a, b*), Gendron (1982), Raymond (1984, 1987), Tucker & Allen (1988) and Weale *et al.* (1988). In an important contribution to the subject, Endler (1978) has argued that the coloration of morphs may in fact represent different ways of being cryptic in a heterogeneous habitat. The polymorphism is selectively neutral when each morph is perceived by the predator as resembling a different random sample of the background.

The evidence now available suggests that the magnitude of apostatic selection is actually increased when morphs are on a heterogeneous matching background. In an experiment with wild birds at a single site, orange and grey pastry baits were made inconspicuous by scattering them over a sheet of hessian partially covered with equal numbers of orange and grey stones (Cooper 1984*a*). In other trials the same prey were made conspicuous by using either equal numbers of lilac and yellow stones (two elements but non-matching) or green stones alone (one element and non-matching). Seventeen prey frequencies were presented on each background in a random order. By regressing a selection coefficient (Manly 1973) on prey frequency,

Cooper detected weak (and statistically insignificant) apostatic selection for each of the controls but a much stronger, statistically significant, effect from the matching background. Cooper's experiment used many birds but he did not obtain separate data from known individuals. Bond (1983) and Gendron (1982), on the other hand, used fewer birds (pigeons and quail respectively) but studied intensively their choice of food (grains and baits) on matching and non-matching backgrounds. Apostatic selection was again more pronounced when the prey were inconspicuous. Similar results have been obtained for human subjects using a light-pen to eliminate dimorphic computer-generated images on a monitor (Tucker & Allen 1988). There is also evidence that anti-apostatic selection is also stronger when the prey match the background (see below).

There are at least two possible reasons why apostatic selection is more pronounced when the prey are on matching backgrounds. First, the higher encounter rate with common prey may make it easier for predators to discriminate common prey from matching non-prey (Bond 1983; Cooper 1984*a*; Staddon & Gendron 1983; Cook 1986). This mechanism is similar to the long-established model for selection on Batesian mimics (Greenwood 1986; Cook 1986). Second, the sensory input from the background heterogeneity may simply create 'noise' that forces the predator to select more apostatically, perhaps indirectly by lowering the encounter rate (Bond 1983; Cooper 1984*a*; Cook 1986). Note that only the first mechanism implies search image, or something akin to it (although see Staddon & Gendron 1983). In their discussion on whether predators detect cryptic prey by forming search images or by slowing down their search rate, Guilford & Dawkins (1987) suggest that search image formation can lead to frequency-dependent selection on polymorphic prey, whereas slowing the search rate will not (although Gendron & Staddon (1983) show that potentially apostatic selection can occur when a predator adopts an optimal search rate while searching for two prey types that differ in conspicuousness). The prediction of Guilford & Dawkins (1987) is testable and this should, they claim, produce good evidence for or against the search image hypothesis. Indeed it should, provided the experiment controls for the 'noise' factor.

The nature of the relation between polymorphism and background is clearly critical to a discussion of frequency-dependent selective predation, and is explored in more depth by Endler (1984 and this symposium).

Density

Extrapolating from the work of Tinbergen (1960) on titmice, Clarke (1962*a*) suggested that apostatic selection should be strongest at intermediate densities and weakest at very high and very low densities. The degree of polymorphism in the tropical African snail *Limicolaria martensiana* does seem to be directly correlated with population density (Owen 1965; Greenwood 1969). However, in general there is no consistent evidence that colour polymorphism and density are so related in other land snails (Cain 1983). This does not necessarily invalidate apostatic selection. It could be that our estimate of prey density is not always the same as the density of prey actually available to the predator, particularly when the habitat is structurally complex.

In our first experiments with green and brown baits (Allen & Clarke 1968) the density of 2 m⁻² was chosen for reasons of practicality. Because it produced a satisfactory response we have also used it in many of our later experiments (Allen 1974, 1976, 1984; Raymond 1984). The effect of changing the density, with one exception, remains unclear. Attempts to measure selection by wild birds when offered a random sequence of frequency and density combinations

at a single site have produced inconclusive results (J. A. Allen, unpublished results; Raymond 1987), possibly because the effects of learning were carried over from one trial to the next. Horsley (1978) avoided this problem by using different birds for each combination of frequency and density and blamed his lack of consistent results on the heterogeneity of behaviour among sites.

By contrast, the strength of apostatic selection by captive quail feeding on red and blue baits did seem to change with density (Cook & Miller 1977) and was strongest at intermediate densities (2.5 m^{-2}). It was virtually absent at the highest density (7.5 m^{-2}) and a frequency-independent preference for red was the more important selective factor. In a series of experiments with domestic chicks and coloured chick crumbs, Willis *et al.* (1980) found that the strength of the frequency-independent component of selection varied with density but could detect no consistent frequency-dependent effect. The degree of apostatic selection by humans searching for inconspicuous images on a monitor appears to be inversely related to density (G. M. Tucker, unpublished results).

It is clear that more work is needed to resolve the effect of prey density on the magnitude of apostatic selection. However, in one respect we are fairly certain: at very high densities the frequency-dependent selection changes direction.

ANTI-APOSTATIC SELECTION

When birds at a single site were presented with 9:1 ratios of green and brown baits at a density so high that they were virtually touching one another, the results seemed unequivocal: disproportionately more of the rare form was taken, regardless of colour (Allen 1972). Two populations were presented simultaneously in sieves placed 1 m apart on the ground; one contained green nine times as common as brown and the other had brown nine times as common as green. The result, for a density equivalent to $10\,577 \text{ m}^{-2}$, was opposite to what had been found for a 'low' density of 2 m^{-2} (Allen 1976). The selection was still frequency-dependent but in the sense that prey fitness increases with increasing frequency. In nature it would eliminate variability from prey populations.

Harvey *et al.* (1974) argued that the results could be explained by the pooled predation by birds selecting in an apostatic manner when first visiting a sieve, developing a preference for the colour which was common and continuing to take the same colour, now rare, when they transferred to the second sieve. Repetition of the experiment with the populations 1 km apart seemed to confirm this explanation, because selection was found to be apostatic on each population, and the chances of birds moving between sites were negligible. On the other hand, observations of captive individual blackbirds in a repeat of the original sieve experiment have failed to provide any evidence that birds prefer the common colour in a tray at the start of a session of feeding (Allen & Anderson 1984). Moreover, using a variety of methods, Horsley *et al.* (1979) have shown convincingly that the original interpretation was correct. For example, in one series of experiments they used the same design as had been used for low density '9:1' populations (Allen 1976). At each of six sites a population with green common was presented for several days, followed by a population with brown common; at another six sites the populations were presented in the reverse order. In all twelve cases selection against brown was stronger when brown was rare.

Using a rather different approach, we attempted to circumvent the criticisms of Harvey

et al. (1974) by presenting, not two 9:1 populations simultaneously, but five, each with a different pair of colours (Allen & Anderson 1984). After about one month the proportions in each container were reversed and predation was recorded for another month. A second experiment was done simultaneously at a second site with the populations presented in the reverse order. For a given pair of colours selection was always anti-apostatic, no matter whether the comparison between frequencies was made within or between sites. More recently, Raymond (1987) has shown that wild birds prey anti-apostatically when feeding on populations of striped and unstriped baits at a density of 30 m⁻². There is also evidence that laboratory mice prefer the rarer scent when given a choice of pellets adulterated with culinary essence (Greenwood *et al.* 1984*a, b*).

What is the proximate cause of anti-apostatic selection by wild birds at high prey density? To the human eye, the explanation seems (literally) obvious. The rare form appears conspicuous against the background of the common form and if the same applies to birds then rare colours may therefore be more likely to be attacked. We know that wild blackbirds do tend to detect monomorphic brown or green baits more quickly when on a background that makes them conspicuous (Lawrence 1985*a, b*) and we also know that wild birds of various species prefer the conspicuous colour when given a choice of equal numbers of green and brown on a background that matches one of them (Allen *et al.* 1987). Although recognizing that a preference for conspicuous rare forms is the most likely explanation for the anti-apostatic selection observed in these experiments, Horsley *et al.* (1979) comment that it is confounded by the results from an experiment at 21 sites, in which five frequencies of green and brown were presented at 800 m⁻². Selection was once again anti-apostatic, despite the fact that the grassy substratum composed 96% of the 500 mm × 500 mm experimental area at each site. It is suspected, however, that some birds are capable of perceiving targets scattered over a wide field of view: wider than that of humans (Blough 1979). If they can immediately 'take in' all the baits within an area 0.25 m² then rare forms may still be perceived as conspicuous.

Further insight into the behavioural basis of anti-apostatic selection by wild birds has been provided recently by an extensive series of experiments at forty different sites (Lochead & Greenwood 1988). In some experiments they presented 9:1 ratios of two shades of green baits scattered over an artificial grass mat coloured either a matching green or a contrasting straw yellow (bait density 617 m⁻²). In other experiments they used 9:1 ratios of two shades of straw-coloured baits on the matching straw-coloured mat and the contrasting green mat. If the 'conspicuousness' hypothesis is correct we might predict that anti-apostatic selection should have been more pronounced when the prey contrasted with the background. In fact, although selection tended to be anti-apostatic overall, the effect was strongest when the baits matched the background.

An alternative proximate cause of anti-apostatic selection (and Greenwood (1984) provides others) relies on the belief that wild birds are conservative in their choice of colours from dense patches. Observations on three blackbirds in a large outdoor aviary showed that each bird would tend to select one colour alone, taking a disproportionate number of this colour regardless of whether it was common or rare (Allen & Anderson 1984). Occasionally this 'transient preference' (E. S. Lawrence, personal communication) would reverse, so that the bird would now prefer the second colour. Overall the behaviour results in anti-apostatic selection. The ultimate significance of such conservative behaviour is unclear, although it could perhaps be a response to feeding on the most obvious natural example of high density 'baits'

TABLE 3. INVESTIGATING ANTI-APOSTATIC SELECTION ON ARTIFICIAL, SEMI-NATURAL AND NATURAL PREY

(All prey at high density. a.-a.s., anti-apostatic selection. For other abbreviations see tables 1 and 2.)

reference	predators	prey	place	result	comments
			(a) prey artificial		
Allen (1972)	wild birds	baits (2: green, brown)	f	a.-a.s.	only one site used
Allen & Anderson (1984)	blackbirds (<i>Turdus merula</i>)	baits (2: green, brown)	l	a.-a.s.	a.-a.s. not caused by rare prey appearing conspicuous among the common?
Allen & Anderson (1984)	wild birds	baits (2: green, yellow; red, brown; buff, purple; orange, white; blue, grey)	f	a.-a.s.	five pairs of colours presented simultaneously; a.-a.s. on each
Greenwood <i>et al.</i> (1984a)	laboratory mice	rat cake (2: green, brown+scents)	l	a.-a.s.	a.-a.s. based on olfactory cues?
Greenwood <i>et al.</i> (1984b)					
Greenwood <i>et al.</i> (1988)	wild birds	baits (2: red, yellow)	f	a.-a.s.	results opposite to those of Greenwood <i>et al.</i> (1981)
Horsley <i>et al.</i> (1979)	wild birds	baits (2: green, brown)	f	a.-a.s.	four series of different designs, at 42 sites
Lochhead & Greenwood (1988)	wild birds	baits (2: 2 shades of green; 2 shades of straw colour)	f	a.-a.s.	40 sites used; a.-a.s. stronger when baits matched the background
Raymond (1987)	wild birds	baits (2: striped, plain)	f	a.-a.s.	—
			(b) prey natural or semi-natural intraspecific variants		
Landeau & Terborgh (1986)	bass (<i>Micropterus salmoides</i>)	silvery minnows (<i>Hybognathus nuchalis</i>) (2: natural brown, dyed blue)	l	a.-a.s.	—
Mueller (1968)	hawks (<i>Falco sparverius</i> and <i>Buteo platypterus</i>)	laboratory mice (2: white, grey (dyed))	l	a.-a.s.	background unimportant
Mueller (1975)	(as above)	(as above)	l	'negative' t.b.	hawks chose unfamiliar colour
Ohguchi (1978)	sticklebacks (<i>Gasterosteus aculeatus</i>)	water fleas (<i>Daphnia magna</i>) (2: yellow, red)	l	a.-a.s.	degree of a.-a.s. increased with increasing prey movement
Ohguchi (1981)					
Pielowski (1959)	goshawks (<i>Accipiter gentilis</i>)	domestic pigeons (<i>Columba livia</i>) (2: light, dark)	f	a.-a.s.	—
Pielowski (1961)					
Wilson & Allen (1988)	wild birds	fly maggots (<i>Calliphora vomitoria</i>) (2: yellow dyed, red dyed)	f	a.-a.s.	a.-a.s. stronger when maggots moving

that many of the birds (particularly blackbirds) are likely to encounter: clusters of berries and other succulent fruits. Each clump of ripe fruits on a plant is usually 'monomorphic' and those variants that do occur tend to be fruits that are unripe. Birds would rarely need to switch between colours when feeding within such a patch.

There is considerable evidence for anti-apostatic selection in experiments with high densities of live prey (table 3). Classic among these is the demonstration that goshawks (*Accipiter gentilis*), when attacking flocks composed of light and dark coloured pigeons, killed disproportionately more of the rare birds (Pielowski 1959, 1961), an effect that has since been supported by work with captive raptors (Mueller 1968, 1971, 1975). Oghuchi (1978, 1981) has demonstrated similar selection by sticklebacks (*Gasterosteus aculeatus*) on swarms of normal and red water-fleas (*Daphnia magna*), as have Landeau & Terborgh (1986) for bass (*Micropterus salmoides*) on dyed and undyed minnows (*Hybognathus nuchalis*). All these examples refer to highly mobile prey in dense groups. It is assumed that predators are, at least momentarily, 'confused' when faced by such a mass of independently moving targets, and that this decrease in the risk of predation could be one of the causes of the aggregatory behaviour in the prey (Welty 1934; Curio 1976). A predator would thus tend to attack an 'easy' target, for instance an individual that stands out by dint of its behaviour or coloration. It seems unlikely that this could be the explanation for the results from experiments with sedentary pastry baits, but it raises the intriguing possibility that the strength of anti-apostatic selection might increase if the baits were imparted with independent movement.

As far as I am aware, no-one has managed to devise a satisfactory method for making a moving swarm of pastry. We have, however, obtained some preliminary data from predation by wild birds on dense aggregations of maggots (*Calliphora* larvae) on a bird table (Wilson & Allen 1988). We used red-dyed and yellow-dyed maggots of a standard size. The speed of locomotion was changed by altering the ambient temperature and we did this by doing the experiments in the winter with or without a night-light candle under the metallic bird table. We used three speeds of movement ('immobile', 'slow', and 'fast'). The first two were obtained by doing the experiments, with the night-light unlit, when the outdoor temperature was below 3 °C ('immobile') and between 3 and 7 °C ('slow'). When the night-light was lit, the surface temperature of the bird table was raised to about 30 °C, depending on the outdoor temperature, and the maggots moved 'fast'. We used two reciprocal 9:1 maggot frequencies for each speed, and four separate sites for each combination of frequency and speed. Selection was anti-apostatic for all three speeds of movement. More crucially, the strength of the anti-apostatic selection increased with the speed of movement, and this interaction was statistically significant.

TOWARDS THE REAL WORLD

In summary, there is good experimental evidence for frequency-dependent selection by predators, although most of this is from unnatural polymorphic prey. There is still much to be learned from selection on artificial prey, despite the obvious caution that must be exercised in the interpretation of the results. The proximate and ultimate causes of both apostatic and anti-apostatic selection are far from understood, and much more information is needed on the effects of morph number, prey coloration, palatability (and profitability), degree of crypsis and density. We need to know the effects of rate of predation in time and of total number of prey consumed (Greenwood & Elton 1979). Information is needed on the effects of different visual

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conditions and the relative importance of predators with different visual systems (Endler 1986 and this symposium). Perhaps above all, we need to know the extent to which behaviour that leads to apostatic selection is widespread among predators.

The experiments can be graded according to their degree of 'naturalness'. Clearly the closer the prey are to real morphs and the closer the predator is to a natural predator of these morphs then the more meaningful the experiment. Experiments with captive predators and natural polymorphic prey in controlled conditions could provide useful information, particularly on behaviour (and G. M. Tucker (unpublished results) has recently obtained some evidence for apostatic selection by four captive songthrushes feeding on artificial populations of live *Cepaea hortensis*).

Our ultimate goal is the detailed investigation of selection by free-ranging predators exploiting real populations of real prey. Quite apart from the obvious practical difficulties, there are two hurdles in the way. First, we would need to have sufficient general knowledge of frequency-dependent selection by predators to be certain we were measuring the appropriate variables. As we have seen, experience with 'prey' of varying degrees of naturalness is steadily increasing our knowledge. Second, if apostatic selection, combined with frequency-independent forces, is indeed maintaining polymorphism in a given population then the morph frequencies are likely to be in equilibrium and selection by the predators would be difficult to detect. This problem could perhaps be overcome by perturbing the existing frequencies (and Reid (1987) has recently obtained evidence for apostatic selection by using this technique on two morphs of a mangrove snail). The alternative is to establish new populations with known frequencies. Bantock *et al.* (1975) did just this by setting up a mixed artificial colony of *Cepaea hortensis* and *C. nemoralis*, although their main aim was to examine the effects of selection for size. They obtained evidence that songthrushes selected against the common morph but could not discount the possibility that this was a frequency-independent effect. A much more substantial series of experiments on *Cepaea* was done by R. W. Arnold (unpublished results), and involved the transplantation of many thousands of snails to new sites. The results proved difficult to analyse but were encouraging. Further experiments of this sort would seem a logical next step in our gradual advance towards testing apostatic selection in the wild.

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Discussion

J. J. D. GREENWOOD (*Department of Biological Sciences, University of Dundee, U.K.*). With reference to the effect of how well the prey match the background, it is important, even though they may only be extremes in a continuum, to distinguish between cases where the prey are easy to detect but difficult to discriminate from elements of the background that they resemble from those where the prey are simply difficult to detect because they blend into the background. These correspond to what Endler (1981) has referred to as 'masquerade' and 'crypsis' respectively. Cooper's (1984*a*) experiment seems to be a case of masquerade. Deborah Lochhead and I (in preparation) have done an experiment with wild birds and cryptic prey and have also found that the frequency dependence is more marked when the prey more closely resemble the background.

Reference

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J. A. ALLEN. I agree that it is important to try to distinguish between crypsis and masquerade (Allen & Cooper 1985). I also agree that the two cases may be extremes in a continuum, and that the relation between the prey and the background in Cooper's (1984*a*) experiment was probably towards the 'masquerade' end of the range. Cooper's prey closely resembled the discrete background elements in their colour but not in their shape and size. It is encouraging to hear that frequency-dependent selection by wild birds is again more pronounced when the prey are properly cryptic.

Reference

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