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Frequency-Dependent Predation, Crypsis and Aposematic Coloration [and Discussion]

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Frequency-dependent predation, crypsis and aposematic coloration

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Frequency-dependent predation may maintain or prevent colour pattern polymorphisms in prey, and can be caused by a variety of biological phenomena, including perceptual processes (search images), optimal foraging and learning. Most species are preyed upon by more than one predator species, which are likely to differ in foraging styles, perceptual and learning abilities. Depending upon the interaction between predator vision, background and colour pattern parameters, certain morphs may be actively maintained in some conditions and not in others, even with the same predators. More than one kind of predator will also affect stability, and only slight changes in conditions can cause a transition between polymorphism and monomorphism. Frequency-dependent selection is not a panacea for the explanation of variation in animal colour patterns, although it may be important in some systems.

Introduction

Animal colour patterns are used in various ways, including protection from predators, communication with conspecifics and thermoregulation. These functions may act together or in opposition (Endler 1983; Brakefield 1985; Reid 1987), so colour patterns may or may not be compromises of these functions (Endler 1987). Frequency-dependent selection of colour patterns (and other traits) can result from the behaviour of predators (Allen, this symposium; Greenwood 1984), the behavioural and genetic processes of courtship, sexual selection and aggression (Partridge, this symposium; Majerus, this symposium; Harper & Maynard Smith, this symposium), and possibly from the behaviour of prey (Paulson 1973; Arnason 1978). This paper will be restricted to the frequency-dependent effects of visually hunting predators on cryptic and aposematic colour patterns. Absolute density can be at least as important to predation as frequency (Greenwood 1969), so the phrase 'frequency-dependent selection' will be used loosely, to include density-dependent selection. Frequency-dependent selection can affect the evolution of colour patterns in various ways, including both favouring and resisting genetic polymorphism (Fisher 1930; Greenwood 1984). The purpose of this paper is to review some of these effects and suggest avenues of further research.

An encounter between a predator and a prey can stop at any stage of the sequence: detection–identification–subjugation–consumption (Endler 1986). A colour pattern can prevent detection, prevent identification as an edible prey or signal to a potential predator that the prey has defences which operate during subjugation or consumption. A colour pattern is cryptic if it minimizes the probability of detection against the visual background. A prey's coloration is aposematic if it is conspicuous and aids the predator to identify the prey as carrying a defence worth avoiding. Post-identification defences can include distastefulness or noxiousness, speed and other behavioural, biochemical or mechanical mechanisms (Wickler 1968; Turner 1984; Pearson 1985; Endler 1986). Although crypsis and mimicry are also defences, for brevity in this paper, the word 'defences' will be used only for post-identification defences.

Crypsis

Animal colour patterns and backgrounds may be regarded as mosaics of patches which vary in size, colour, reflectance and shape. Therefore, to be cryptic, a colour pattern must resemble a random sample of the background colour pattern perceived by predators at the ages, times, visual conditions and microhabitats in which the prey are most vulnerable to predation (Endler 1978). The degree of crypsis may be measured by the similarity between animal and background with respect to the size, colour, reflectance and shape distributions, and conspicuousness is proportional to the divergence in one or more of these distributions. Cryptic and conspicuous coloration are thus extremes of a spectrum of prey colour pattern detectability (Endler 1978, 1984, 1986).

If cryptic colour patterns are random samples of the visual background, and the background consists of many colour patches, then there are many different possible random samples of the same background. Therefore, even if there is strong selection for crypsis on a particular background, many different colour pattern phenotypes (morphs) can do equally well on that background, and different backgrounds are likely to have different combinations of equally cryptic morphs. Varied backgrounds are therefore permissive of colour pattern polymorphisms. But, if the morphs are equally cryptic, then they may drift in frequency (Endler 1978). Cook (1986) modelled a system with two different morphs that mimicked specific single background colour patches and showed that this results in a neutrally stable polymorphism; unless some other selective factor or mutation actively maintains the polymorphism, random genetic drift will result in loss of polymorphism. If morphs do better on their own background colour patch, or there is background patch selection, then the model becomes equivalent to the multiple niche polymorphism models reviewed by Maynard Smith & Hoekstra (1980), and the conditions for a stabile equilibrium are relatively stringent. The conditions are less stringent if there is habitat choice for background patches against which the morphs are most cryptic, or if the predators exercise frequency-dependent selection (Cook 1986; Maynard Smith & Hoekstra 1980). It would be interesting to know how different the results would be if the prey were modelled as random samples of the background, but containing more than one colour patch as envisioned by Endler (1978, 1984), rather than as the single patches of Cook (1986).

The difference between a cryptic colour pattern being a random sample of a single (Cook 1986) or many (Endler 1978, 1984) background patches may affect colour pattern variation. If a colour pattern polymorphism is selectively neutral on a visual background with very many different colour patches, then genetic drift will prevent or eliminate the correlation between background and animal colour pattern patches predicted by Endler (1978). Cook (1986) found that the correlation only occurs if there is symmetrical selection in which each morph was equally cryptic on its own background patch, and equally uncryptic on the other patches. Such symmetry does not seem very likely. On the other hand, if an animal's colour pattern consists of many of the background colour patches, then it must have combinations of colours which are common in the background, as well as common colours (this argument also applies to patch sizes, reflectances and shapes (see Endler 1978)). Survivors of predation will have combinations of colours that are characteristic of the background because unusual combinations will appear more conspicuous and will be disproportionately eaten. This will give rise to a correlation between the animal and background colour patterns, even though the morphs carrying different colour combinations may be subject to genetic drift. Such correlations have been found in moths (Endler 1984) and mangrove snails (Reid 1987). This also predicts that more complex backgrounds (backgrounds with more and more different kinds of colour patches) will have more and more extensive colour pattern polymorphisms than simpler backgrounds (Endler 1978, 1984). Support for this prediction comes from the temporal change of moths and background colour patterns in a New Jersey deciduous forest, although the parallel changes involve species rather than morphs within species (Endler 1984). These ideas have not been tested for fast moving prey, but may still apply perpendicular to the axis of movement, and with colours and patches blended by motion (Endler 1978, 1980). In any case, it is likely that the colour pattern parameters of the background affect the morph frequencies and even the equilibrium caused by frequency-dependent selection (Cook 1983; Endler 1984; Hughes & Jones 1985; Reid 1987). More experimental work is needed on colour pattern polymorphisms on backgrounds with many different kinds of coloured patches; this is characteristic of natural backgrounds.

A predator searching for cryptic prey tries to detect objects that deviate in some way from the background colour pattern. The probability of detection may be proportional to the deviation, and the latency to detection is proportional to the degree of crypsis (Endler 1986). If a predator searches for a prey species that has two or more morphs that are equally cryptic, then it may modify its perceptual and cognitive systems in such a way that it can detect one morph more easily than the others. This transitory enhancement of detection ability for a given colour pattern is called a *search image*. It is assumed to be some function of selective attention to certain visual cues (Bond 1983; Lawrence & Allen 1983; Gendron 1986; Allen, this symposium) or learning a template for selective pattern recognition. If the search image for a given morph is created faster and retained longer for higher encounter (detection) rates, then that morph's fitness will decline with increasing density. If the formation of a search image for one morph reduces the quality or retention time of a search image for another morph, then the fitness of a morph will depend upon both its density and frequency. In both cases a morph will be at a relative advantage when rare and at a relative disadvantage when common. This kind of frequency-dependence is known as *apostatic selection* and can maintain colour pattern polymorphisms (reviewed in Allen, this symposium; Clarke 1962, 1969; Greenwood 1984).

The existence of search images is controversial, and in fact the direct evidence is quite ambiguous (Guilford & Dawkins 1987). But predators do cause apostatic selection (Greenwood 1984; Allen, this symposium). What other explanations are possible? One possibility is that the frequency-dependence occurs during the identification rather than the detection stage of predation. The decision to attack or not to attack a detected prey may depend upon its frequency (or density), and this may be true even if the probability of detection is independent of frequency. The predators' energetic balance may affect attack decisions. Optimal foraging theory and experimentation (summarized in Stephens & Krebs 1986) show that foraging predators switch between multiple prey types according to their relative benefits and costs, or 'profitabilities'. The benefits and costs of each morph are functions of their food values, densities (which affect encounter rates and foraging times), handling times, and risks to the predator during the latter stages of the predation sequence. The relative profitability of morphs detemines which morph or morphs should be attacked when detected. Of two prey types, the currently less profitable prey should start to be attacked when the encounter (and detection) rate of the more profitable prey is less than a threshold (Stephens & Krebs 1986). The switch in preference may be all-or-none (Stephens & Krebs 1986) or partial (Getty & Krebs 1985), depending upon the physiology and behaviour of the predator. If the post-detection defences of the morphs, which determine their handling times and other costs, remain constant, then their profitabilities will increase with their relative frequencies, and their fitnesses will decline. Even if defences remain constant, predators may learn to mitigate some of them. If attack skills depend upon practice, then the more frequent morphs will be at an additional relative disadvantage: a morph gives the predator more practice as it becomes more common. For both reasons, post-detection choice can lead to apostatic selection, even in the absence of search images.

A predator can reduce the need to make decisions after detection by foraging in places that have a higher density of a morph, and hence a greater discovery rate. It should spend more time trying to detect cryptic prey in a habitat patch when the morph density increases to a profitable level, and this will also result in apostatic selection (Gendron & Staddon 1983; Getty & Krebs 1985; Guilford & Dawkins 1987). Skills may also be developed for patch choice, further increasing the frequency-dependence.

The degree of crypsis can effect the search costs of the predator and further alter the frequency-dependent relation. For example, Gendron & Staddon (1983) showed that if we assume that the probability of detecting a prey is inversely related to search rate as well as to the degree of crypsis, then the optimum search rate represents a balance between prey detection and encounter rate (potential maximum detection rate). The degree of crypsis affects the predator's optimal search style in that as the prey become more cryptic the search rate drops. If there are two morphs with differing crypsis, then the optimal search rate increases with the frequency of the less cryptic morph, which in turn may result in a rapid drop in the probability of taking the more cryptic morph. Thus there can be an interaction between detection efficiency and foraging decisions. This needs more work.

For brevity, and because they are a subset of all possible modes of optimal foraging, the processes of energetic- and skill-based foraging decisions will be referred to as *judicious foraging*. As a result of this kind of optimal foraging, the likelihood of a decision to attack a given morph after detection, or to search in a place where that morph is most common, may increase with the morph's frequency, leading to apostatic natural selection and a stable equilibrium of morph frequencies. The behavioural evidence for search images is equally consistent with optimal foraging explanations for apostatic selection (Guilford & Dawkins 1987). In summary, both neural (search images) and energetic (judicious foraging) processes can lead to apostatic selection.

Because search image formation and judicious foraging can yield the same observed predator behaviour, it may be difficult to determine the causes of a particular case of observed apostatic selection (Guilford & Dawkins 1987). But the distinction is important because apostatic selection does not necessarily result from judicious foraging. The details of the optimal predator behaviour, and the form of the frequency-dependent relation, depend upon the distribution and properties of the prey. Depending upon these parameters, the fitness of a morph may decrease, remain about the same, or even increase with frequency (Hubbard *et al.* 1982; Greenwood 1984, 1985; Getty & Krebs 1985; Guilford & Dawkins 1987). If the fitness increases with frequency, this is known as *anti-apostatic selection* (Greenwood 1985; his term 'pro-apostatic selection' is synonymous with apostatic selection, and so will not be used here). For example, if the density of the prey species is high, there may be anti-apostatic selection, whereas if it is low, then there may be 'normal' apostatic selection (Cook & Miller 1977; Greenwood 1969, 1984, 1985; Horsley *et al.* 1979; Willis *et al.* 1980; Cooper 1984; Allen & Anderson 1984).

The effect of density on the sign and magnitude of frequency-dependent selection can occur without search images or judicious foraging. If the prey density is low, then the visual background of a particular prey individual is unlikely to be near other individuals, and apostatic selection can operate as it is assumed to. If the prey density is high, then the background of a particular individual may include another individual. If the prey density is very high, as in species which aggregate or school, then the visual background is essentially the prey species rather than inanimate objects. If the prey are their own backgrounds, then the common morph has an advantage because it will be cryptic against the common morph, whereas the rarer morphs will be at a disadvantage because they will be conspicuous against the commoner morph. This is one explanation for the low variance in colour pattern and frequent lack of sexual dimorphism in schooling and aggregating species that are not aposematic. If density is high enough, there may be a confusion effect as well as selection against oddity, and the confusion of so many moving prey may increase the disadvantage of the rarer form even more (Horsley *et al.* 1979; Greenwood 1984; Landeau & Terborgh 1986).

There are three more explanations for apostatic selection which do not require either search images or judicious foraging: aversion to rare forms, learning to recognize food, and digestion efficiency. Many different vertebrate predators have an aversion to prey that are rare or which are unfamiliar, and a preference for prey with which they are familiar (Coppinger 1969, 1970; Bryan 1972; Vaughan 1983; Cooper 1984; Schlenoff 1984; Allen & Anderson 1984; Allen, this symposium). Vaughan (1983) found that birds are startled more often when they encounter rarer than common prey that they have seen before, and are even more likely to be startled by novel prey. Schlenoff (1984) found that, when birds have had unpleasant experiences with other unusual prey, they will be startled at any unfamiliar prey, regardless of whether or not it is distasteful. The startle response may give a prey additional time to escape. Aversion to rare morphs will usually lead to apostatic selection. Learning to detect and to recognize prey will have similar effects. A morph that is common will be encountered earlier by an inexperienced predator and therefore may be learned to be recognized as a food item faster than a rare morph. For an especially cryptic morph, a young predator will have more encounters to learn to detect a common morph from the background compared to a rare morph (Cooper 1984). Both aspects of learning will usually lead to apostatic selection. If many encounters are required to learn to detect a cryptic prey from the background (whether or not there is search image formation), we expect the strength of apostatic selection to be greater for more cryptic compared with less cryptic prey, and there is some evidence for this (Cooper 1984). Finally, it is possible that individuals may get better at digesting items currently in their diet (L. Partridge, personal communication, 1987). If this leads to diet preferences (as does emesis in the learning of jays feeding on monarch butterflies (Wickler 1968)), then the effect will be apostatic. Greenwood (1984) gives an excellent review of the various reasons for predators causing frequency-dependent selection. In summary, depending upon the relative profitabilities of cryptic prey, there may be apostatic or anti-apostatic selection, and the prey may be polymorphic or monomorphic.

Except for the excellent papers by Hubbard *et al.* (1982), Gendron & Staddon (1983), Getty

& Krebs (1985), Greenwood (1984), Leimar *et al.* (1986) and Guilford & Dawkins (1987), there has been virtually no attempt to examine the implications to prey of optimal foraging by predators. Leimar *et al.* (1986) used an Evolutionary Stable Strategy (ESS) approach to investigate stability of cryptic or aposematic coloration and optimal foraging by the predator, but aside from this, there are as yet no models considering the joint evolution of predatory foraging behaviour and prey morph (or allele) frequencies.

Aposematic coloration

Aposematic coloration adds a post-detection defence to conspicuous coloration, and aims to produce an association between the colour pattern and the predator's memory of previous encounters with the defence. In considering the evolution of aposematic coloration, it is important to make the distinction between the evolution of conspicuousness and the evolution of the defence (Harvey & Paxton 1981).

It is possible for predators to learn to avoid defended prey that are cryptic, but cryptically defended species are relatively uncommon. Why are aposematic colours usually conspicuous? Experiments have shown that it takes predators less time to learn to avoid more conspicuous compared with less conspicuous distasteful prey (Goodale & Sneddon 1977; Gibson 1980; Gittleman & Harvey 1980; Vaughan 1983; Sillén-Tullberg 1985), and this also applies to palatable prey (Cooper 1984). This may result from either greater detection efficiency or more rapid decision making, because for greatest efficiency, aposematic coloration must be easy to detect, easy to recall and easy to associate with the defence. In addition, a conspicuous colour pattern may be detected from a longer distance than a cryptic colour pattern (Smith 1974; Endler 1978; Guilford 1986; Guilford & Dawkins 1987). If predators make mistakes in attacking colour patterns that they think are unpalatable, a longer distance between detection and the prey gives the predator more time to decide to attack, therefore presumably leading to fewer mistakes. If the number of mistakes declines with the conspicuousness of a defended morph, then conspicuous morphs will increase in frequency and more cryptic morphs will decline (Guilford 1986). Fewer mistakes also increase the predator's foraging efficiency, so conspicuous aposematic coloration may also involve coevolution. For these reasons, conspicuous coloration is strongly favoured when a species has a post-detection defence.

The initial stages of spread of a conspicuously defended morph in a population of inconspicuous defended morphs is somewhat problematical because at frequencies that are low enough there will not be enough of the conspicuous morph to train the predators, and their greater conspicuousness may actually favour the more cryptic morph. There are several ways to overcome this problem. (1) Random processes may increase the frequency of the rare conspicuous morph (Mallet & Singer 1987). (2) Aggregations of kin (Leimar *et al.* 1986), siblings, or similar genotypes carrying the rare allele (Guilford 1985), may increase the effective local density of the rare morph. (3) Reluctance of predators to take novel and rare forms, and other apostatic effects (§2) may increase the frequency of the rare morph. Search images can apply to aposematically coloured prey as well as to cryptic prey; the decision to attack after detection is all that is affected by the defence. (4) Predators may recognize the more and less cryptic morphs as the same defended species because they differ only slightly at the early stages of the evolution of aposematic coloration. (5) Natural populations may vary enough in crypsis (Endler 1984) so that initially the less cryptic morph may already be at a high enough density for predator training to be possible. These possibilities need more investigation.

It is reasonably clear how species with post-detection defences evolve conspicuous aposematic coloration, but the evolution of the defence itself is more of a problem. If a defence carries a risk which is low enough so that some prey escape to later reproduce, then natural selection will favour it. But, as Fisher (1930) first noticed, how does a defence such as distastefulness evolve when a prey must be killed to be tasted? Wicklund & Jàrvi (1982) suggest that, because many aposematic species are tough and difficult to kill, that toughness will reduce the risk of attack, and allow enough distasteful individuals to escape to favour distastefulness. But this only begs the question: how does toughness evolve? The problem is especially difficult if the defence effect is emetic, and does not act until several hours after ingestion. The fundamental problem is: how can natural selection favour a defence that operates during or after the killing phase of predation?

Because many distastefully aposematic species aggregate, kin selection is a reasonable explanation; the inclusive fitness of a distasteful morph will be higher than a palatable morph (Fisher 1930; Harvey & Paxton 1981; Harvey *et al.* 1982; Leimar *et al.* 1986). For example, if a bird attacks an aggregation of *Malacosoma* moth larvae and eats one or two of the larvae and thereby learns to avoid that colour pattern in the future, this reduces the likelihood that it will attack the aggregation again. This protects the siblings because aggregations tend to consist of individuals from the same egg mass. There is some argument about whether or not this is kin selection, because the mechanism will work whenever similar colour pattern genotypes aggregate, whether or not they are kin (Guilford 1985). For example, Müllerian mimics are protected by each other even when they are in different orders. Sillén-Tullberg & Bryant (1983) provided a graphical model of the evolution of aposematic coloration that does not require kin selection. It is essentially a model of optimal foraging on prey that are tough enough to survive some attacks, as in Wicklund & Jarvi (1982). It may apply generally to the advantage of any post-detection defence, where the presence of an existing defence will aid the spread of a new one. Although the conditions of this model are more restrictive than those of the kin selection models, it may explain the presence of aposematic coloration in solitary or other non-aggregating species. The enhancement of defences later in the predation sequence by defences earlier in the sequence may also explain why aposematic coloration is frequently associated with a suite of mechanical, gustatory and biochemical defences. The evolution of suites of defences is clearly both frequency- and density-dependent, and well worth further investigation. Leimar *et al.* (1986) provide a good review and a general model of the evolution of aposematic coloration and post-detection defences under a variety of biologically realistic conditions.

Vaughan (1983) and Brower *et al.* (1971) noted that certain colours, such as black and other dark colours, which are not ordinarily thought of as conspicuous, also resulted in faster predator learning. Conspicuousness is increased by increasing the mismatch in total reflectance between animal and background, not just colour contrast (Endler 1978, 1983, 1984, 1986), so these results may also demonstrate the advantage of a conspicuous warning. Colours such as black and yellow are common in a large number of unpalatable species (Wickler 1968), and this may be a function of physics and visual physiology. Certain colours will always be more conspicuous than others under given visual conditions and abilities, for example blue and yellow have the highest signal:noise ratio in shallow marine water whereas red and orange are best in lakes (Lythgoe 1979). These colours will therefore be favoured in a wide variety of aposematic taxa subject to predation in the same visual environment. This needs more investigation, especially in the terrestrial environment. There is also the possibility of innate aversion to certain colour patterns. An interesting example of this is Smith's (1975, 1977) experiments showing that naïve motmots and kiskadees avoid colour patterns that resemble coral snakes (black, yellow and red bands), which would be dangerous for these tropical birds to attack. If the avoidance of conspicuous prey is innate, or purely a function of physiology and the physics of light, then frequency-dependent selection may not be exerted by the predator. The comparative importance of innate against learned aversion to colour patterns will have to be tested directly.

If predator avoidance is affected by learning, and there is more than one prey morph, then selection will be frequency-dependent and anti-apostatic, and the population will soon become monomorphic. This can arise for the same kinds of reasons that favour apostatic selection of cryptic prey: (1) shifts in detection ability with frequency; (2) shifts in decision making as a result of changes in net profitability with frequency; and (3) encounter rates increase with frequency, leading to faster learning and longer retention time of the association between the colour pattern and the defence. If the predator has a limited memory capacity, then this will also favour monomorphism, because it is the retained aversion which increases the prey's fitness. The aversive reaction and the frequency-dependence are proportional to frequency, density and the degree of post-detection defence (Fisher 1930; Estabrook & Jesperson 1974; Bobisud & Potratz 1976; Turner 1984; Turner *et al.* 1984; Arnold 1978; Thompson 1984). If we regard post-detection defences as mechanisms that reduce profitability of prey, then similar predictions are made by optimal foraging (Greenwood 1984; Getty 1985; Stephens & Krebs 1986) and ESS theory (Leimar *et al.* 1986).

The prediction of selection for monomorphic aposematic coloration applies to species as well as to morphs within species; this is essentially the explanation for Müllerian mimicry (reviewed in Turner *et al.* 1984). Batesian mimicry also results in convergence in colour patterns among species, but the fitness consequences to the protected and unprotected forms are qualitatively different: in Batesian mimicry the model's fitness declines as the mimic's frequency increases, whereas in Müllerian mimicry the fitnesses of both prey increase with their frequency. There is a spectrum of relative defence of the two species from equal defence ('pure' Müllerian mimicry) through cases where one is considerably more protected than the other, to cases in which one is not protected at all ('pure' Batesian mimicry). All will favour close resemblance (Turner *et al.* 1984). In addition, in Batesian mimicry, as the density of both model and mimic increases, the profitability of the mimics will increase, and predators may take more time (or neural capacity) to distinguish them from the models, encouraging further convergence. In any case, the relative frequencies and defences of the two prey will affect their profitabilities (Getty 1985; Leimar *et al.* 1986), favouring convergence of colour patterns, hence monomorphism in colour patterns within localities.

In spite of the predictions of monomorphism, some aposematic species are polymorphic, and Thompson (1984) has proposed that these cases may represent a balance between apostatic selection and selection for aposematic coloration, or a balance between frequency-dependent and frequency-independent selection. In his model, the fitness of a morph i depends upon its frequency f_i, the strength of frequency-dependent predation s_i and the strength of frequency-independent selection C_i, or

$$W_i = C_i - s_i f_i. \qquad (1)$$

Apostatic selection predominates for morph i if s_i is positive, and selection for aposematic coloration predominates if s_i is negative. Two or more morphs can differ in both C and s, and Thompson (1984) explores the various possibilities. If there are two morphs ($i = \mathrm{a}$ and b) controlled by a single locus with two alleles and complete dominance, then the equilibrium is

$$\hat{q}^2 = (C_\mathrm{b} - C_\mathrm{a} + s_\mathrm{a})/(s_\mathrm{a} + s_\mathrm{b}), \tag{2}$$

where $\hat{q}$ is the recessive allele frequency at equilibrium. The conditions for a stable and non-trivial ($0 < \hat{q} < 1$) equilibrium are

$$0 < (s_\mathrm{a} + s_\mathrm{b}) < \hat{\bar{W}}/(\hat{p}\hat{q}^3), \quad C_\mathrm{a} > (C_\mathrm{b} - s_\mathrm{b}) \quad \text{and} \quad C_\mathrm{b} > (C_\mathrm{a} - s_\mathrm{a}), \tag{3a–c}$$

where $\hat{p} = 1 - \hat{q}$, and $\hat{\bar{W}}$ is the mean fitness at equilibrium. If the parameters are outside this range, then there may be an unstable nontrivial equilibrium, or uniform selection for monomorphism. Thus, a polymorphism is favoured if (*a*) one morph is favoured because it is aposematic and the other form is not subject to frequency-dependent selection, but has a greater frequency-independent fitness (C_b large), and (*b*) one morph is favoured under apostatic selection and the other favoured under selection for aposematic coloration when the intensity of apostatic selection is greater than the aposematic selection and it is strong enough to result in a non-trivial equilibrium. It is clear that various combinations of the parameters can lead to polymorphism, even when there is selection for aposematic coloration. Conversely, other combinations of parameters could lead to monomorphism even when there is apostatic selection. It would be interesting to know how often these conditions are found in nature and whether or not they apply to polymorphic aposematic species such as ladybirds. An additional explanation that has not received enough theoretical or empirical attention is the possibility that an aposematic species may be polymorphic if the different morphs are members of different sympatric Müllerian mimicry complexes that fluctuate greatly in relative abundance (Brown & Benson 1974; Brakefield 1985). Most cases of polymorphic Müllerian mimicry involve geographical variation, often with hybrid zones between the monomorphic populations. These hybrid zones can move, causing some monomorphic zones to spread at the expense of others (Mallet 1986). This results from anti-apostatic selection at any particular population (Mallet & Barton 1988) making the local polymorphism unstable, and gene flow holding the monomorphic zones together (Mallet 1986). Much remains to be done with aposematic coloration.

Effects of more than one predator

Differences among predators

A prey species is likely to be eaten by many different kinds of predator from a variety of taxonomic groups. For example, a moth may be preyed upon by squirrels, monkeys, birds, snakes, lizards, treefrogs, mantids, beetles, assassin bugs and spiders. The visual abilities (visual acuity, colour vision, etc.) of each predator can be quite different, so a morph that one predator perceives as very cryptic may be perceived by another predator as less cryptic or even conspicuous, and vice versa (Hinton 1976; Endler 1978, 1986). Vision may vary even within species (Neitz & Jacobs 1986; Jacobs & Neitz 1987; Archer *et al.* 1987). In addition, each predator may forage in a different way and under different lighting conditions. For example, some species may forage more at midday whereas others mostly forage in the morning, and even within birds some tropical species forage primarily when the sun is out whereas others forage whether or not the sun is masked by cloud. The visual background (Endler 1978) and the ambient light spectrum (McFarland & Munz 1975; Lythgoe 1979) can be quite different at different times of day, and this is especially true in aquatic environments (Lythgoe 1979) and below the canopy of trees or shrubs (Endler 1978). The visual backgrounds and ambient light conditions in all habitats, but especially aquatic habitats, can also change radically with season (see, for example, Endler 1978, 1984). There are also strong differences in light spectra between adjacent microhabitats within forests and other habitats (Hailman 1979). Thus any differences between predators in vision, foraging time, date or microhabitat may lead to radically different perceptions about the visibility of colour patterns. Predators may also vary in their learning abilities, energetics, hunger and in other ways that will affect diet choice. Such differences may apply between and within predator species, and even within the same predator individual at different times and seasons. Virtually nothing is known about such variation in any predator, or about the interaction between these effects and the evolution of foraging behaviour, phenology or sensory systems.

Müllerian and Batesian mimicry will also be affected by differences among predators. If the strength of the defence of the most well-defended prey increases sufficiently (in evolutionary time) to reduce profitability greatly, then a predator may ignore the entire model mimic system (Estabrook & Jesperson 1974; Arnold 1978). In this case the remaining combination of predators will determine the mimicry dynamics. If the new combination of predators' vision or foraging conditions are very different from the old ones, there may be a large shift in frequencies, a new equilibrium may be reached, equilibrium may be entirely lost, or a new colour pattern may evolve. The effects of different kinds of predator and shifting predator risks on mimicry needs further investigation.

What is the effect of more than one kind of predator on the evolution of colour patterns? How do combinations of predators, which vary in visual abilities and hunting behaviour, affect the presence or stability of polymorphisms? These problems appear to have been neglected in the literature, so the model presented below is a very preliminary attempt to answer some of these questions.

Let us consider a relatively simple system with two kinds of predator feeding on two morphs of the same prey species. Let the total predation by predator 1 be P and the total predation by predator 2 be $(1-P)$, where $0 \leqslant P \leqslant 1$. Let the prey morphs be determined by two alleles (A and a) at a single locus, with A dominant to a. Define the frequencies of A and a to be p and q respectively ($p+q=1$), and assume that the only violations of the Hardy-Weinberg assumptions are caused by predation. The A phenotype (genotypes AA. Aa) will have fitness W_A and the a phenotype (genotype aa) will have fitness W_a, and these fitnesses depend only upon the effects of predation by predators 1 and 2. We will refer to the two phenotypes as morphs.

Frequency-independent selection only

Assume initially that the predators do not exert frequency-dependent selection, but that they perceive the two morphs differently. We will relax this assumption later. For morph A, let c_1 and c_2 be the perceived crypsis with respect to predators 1 and 2 respectively. For morph a, let d_1 and d_2 be the perceived crypsis for the two predators. Let the overall fitness of the two morphs be:

$$W_A = Pc_1 + (1-P)\,c_2 \quad \text{and} \quad W_a = Pd_1 + (1-P)\,d_2. \tag{4a, b}$$

To make calculations simpler, we can work in terms of the crypsis of morph A relative to morph a within each predator. Let $C_1 = c_1/d_1$ and $C_2 = c_2/d_2$. This yields:

$$W_A = PC_1 + (1-P)\,C_2 \quad \text{and} \quad W_a = 1. \tag{5a, b}$$

Note that C_1 and C_2 can vary between 0 and infinity, and that the larger they are relative to unity, the greater crypsis morph A has relative to morph a for the same predator. It is clear that allele A will spread to fixation if $W_A > W_a$, or

$$PC_1 + (1-P)\,C_2 > 1, \tag{6}$$

and allele a will be fixed if the reverse is true ($W_A < W_a$). Let the quantity $PC_1 + (1-P)\,C_2 \equiv C$, then (6) becomes

$$C > 1. \tag{7}$$

The quantity C measures the average relative crypsis of morph A, weighted by the risk due to each predator. If P is large, then predator 1 accounts for most of the risk and so the relative crypsis with respect to predator 1 is more important to fitness than C_2. This makes good sense: if the average crypsis of morph A is greater than one, then allele A will spread to fixation, and the population will become monomorphic for A. Similarly, if $C < 1$, then the population will become monomorphic for a. Note that the predators can have quite different perceptions of colour patterns, but so long as the average crypsis of morph A weighted by the risks of each predator is greater than 1, it will spread to fixation (7). Fixation is possible even if one of the morphs is less cryptic to one predator and more cryptic to the other, again the criterion is merely $C > 1$ (figure 1).

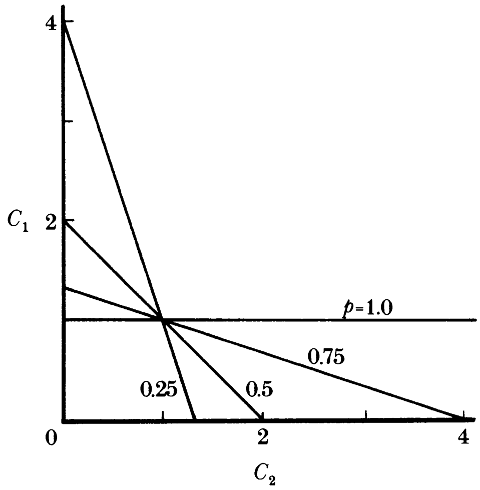

FIGURE 1. Conditions for spread to fixation of one of two morphs, each subject to predators with different vision. C_1 and C_2 are the crypsis of morph A relative to morph a, as perceived by predators 1 and 2, respectively. The Cs can vary from 0 to infinity; $C_i = 1$ means equal crypsis (with respect to predator i) and $C_i > 1$ means that morph A is more cryptic than morph a. P is the proportion of risk of the species from predator 1 and $(1-P)$ is the risk from predator 2. To spread to fixation, the crypsis values of morph A must lie above the line for a given P. As P declines, the crypsis of morph A with respect to predator 1 (C_1) can be less than one but A will still spread to fixation so long as it is counteracted by greater crypsis with respect to predator 2.

It is possible for there to be a neutral equilibrium if the relative crypsis and predator risks exactly balance, so that $C = 1$. This may not be as unlikely as it first appears because the effect of optimal foraging may be to adjust P such that $C = 1$, making the marginal costs equal (Stephens & Krebs 1986; Getty & Krebs 1985). On the other hand, as discussed in §2 and §3, optimal foraging is also likely to result in frequency-dependent fitnesses, so this base model may not apply.

Frequency-dependent selection only

Let the two morphs be equally cryptic to both predators ($C_1 = C_2 = 1$). Assume that the fitness of a given morph is proportional to its frequency; the parameters K_1 and K_2 measure the degree of frequency-dependent selection by predators 1 and 2, respectively. Assume also that the predators do not effect each other's assessment of, or experience with, the morph frequency. The fitnesses are now:

$$W_A = P[1-K_1 f] + (1-P)[1-K_2 f] \tag{8a}$$

and

$$W_a = P[1-K_1(1-f)] + (1-P)[1-K_2(1-f)], \tag{8b}$$

where f is the frequency of morph A and $(1-f)$ is the frequency of morph a; $f = (1-q^2)$ and $(1-f) = q^2$. If positive, K_i indicates that predator i ($i = 1$ or 2) is causing apostatic selection, in which the fitness of a morph declines with its frequency. If negative, K_i indicates that predator i is causing anti-apostatic selection, in which the fitness increases with frequency. In other words, positive K_i indicates apostatic selection, and negative K_i indicates selection for aposematic coloration.

Following Lewontin's (1958) analytical method, there is a single nontrivial ($0 < \hat{q} < 1$) equilibrium at $\hat{f} = 1-\hat{q}^2 = \frac{1}{2}$. The equilibrium is stable if

$$-[PK_1 + (1-P)K_2] < 0. \tag{9}$$

Define the quantity $PK_1 + (1-P)K_2 \equiv K$, the weighted mean frequency-dependence of the two predators. Expression (9) becomes

$$K > 0. \tag{10}$$

Clearly, the equilibrium is stable if both predators exhibit apostatic selection, or the effects of both predators are such that the weighted average selection is apostatic ($K > 0$). The equilibrium is unstable if the weighted average selection of the predators is anti-apostatic (K negative); in that case the allele that is fixed depends upon the initial allele frequency or the direction of random perturbation from the unstable equilibrium. The results are the same as those of Clarke & O'Donald (1964) when $K = K_1 = K_2$ (one predator) and $K > 0$. When $K = K_1 = K_2$ and $K < 0$, the model reduces to a single predator model of selection for aposematic coloration (as described by Thompson (1984)).

Frequency-dependent selection and perceived crypsis differences

I now combine the effects of differences between the predators in frequency-dependence and perceived crypsis. First, consider differences in crypsis ($C_1 \neq C_2$) but no differences in frequency-dependence ($K_1 = K_2 = K$). The fitnesses are now:

$$W_A = C_1 P(1-Kf) + C_2(1-P)(1-Kf) = C(1-Kf) \tag{11a}$$

and

$$W_a = P[1-K(1-f)] + (1-P)[1-K(1-f)] = [1-K(1-f)], \tag{11b}$$

where $C = PC_1 + (1-P)C_2$, as in (7). In contrast to Thompson's (1984) model, the frequency-independent component of fitness (C_i) was multiplied by the frequency-dependent component (compare equations 1 and 11a,b). This yields an equilibrium at:

$$\hat{q}^2 = \{(K-1)C+1\}/K(C+1). \tag{12}$$

The equilibrium is stable if:

$$K > 1-(1/C). \tag{13}$$

Because (12) can take any value, it is necessary to find the conditions for $\hat{q}$ to be between 0 and 1 (non-trivial). They are:

$$K > 1 - C \quad \text{and} \quad K > 1 - (1/C). \tag{14a, b}$$

Note that (14*b*) is the same as (13), so expressions (14*a*, *b*) are the conditions for a stable non-trivial equilibrium. These conditions are summarized in figure 2. Thompson (1984) obtained a similar result in his one-predator model, using a different arrangement of frequency-dependent and frequency-independent (C) fitness components.

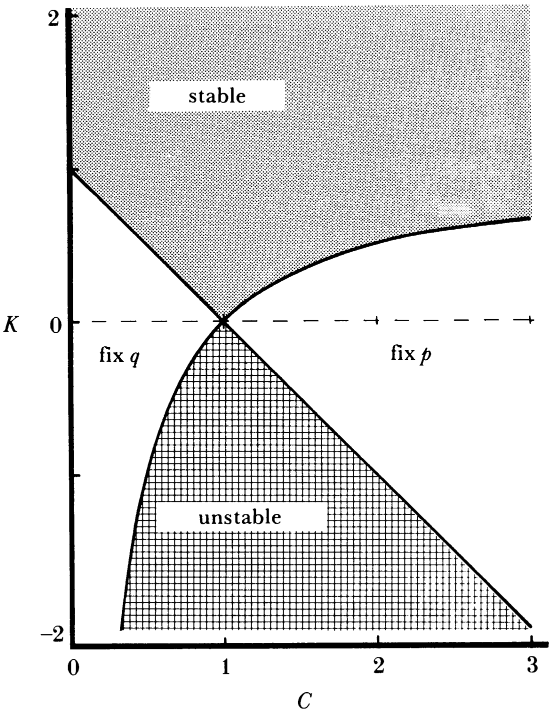

FIGURE 2. Conditions for spread or equilibrium at a prey colour pattern locus when two predators have different perceptions about the prey morph's crypsis (C_1 and C_2) and either the same kind and degree of frequency-dependent selection on the morphs ($K_1 = K_2$), or different selection ($K_1 \neq K_2$) with cov $[C_i, K_i] = 0$. C is the average crypsis and K is the average frequency-dependence, weighted by the relative risk due to each predator. The solid lines are the critical values for a stable non-trivial equilibrium (see text). If the parameters are above both lines (shaded), then there will be a stable non-trivial equilibrium. Elsewhere there will either be an unstable (hatched) or trivial equilibrium. A population is more likely to become monomorphic if there is net anti-apostatic selection ($K < 0$; below the dashed line) or if there is net apostatic selection ($K > 0$) and large differences in crypsis (C very different from 1). Conditions for stability are less restrictive as K increases.

If there is apostatic selection ($K > 0$) and if $K > 1$ then there will be a stable equilibrium, provided that C is not very large. If there is apostatic selection such that $0 < K < 1$, then there will be a stable equilibrium provided that C is not too large or too small, and the conditions are less stringent for larger K (figure 2). Recall that C is a measure of relative crypsis, and the more different it is from 1 the greater the difference in average conspicuousness between the morphs. This makes intuitive sense because the greater the difference in crypsis the more the predators favour one morph over another, and the more difficult it is for apostatic selection to maintain the polymorphism. This result also makes an interesting prediction: if $0 < K < 1$ is frequent in nature, then we are more likely to see colour pattern polymorphisms with morphs which are not very different from one-another with respect to their conspicuousness (measured as in Endler (1984)), and we are unlikely to see polymorphisms with morphs that differ greatly in degree of crypsis. This appears to be true from the literature, but we need extensive quantitative data to test this prediction directly. Allen & Anderson (1984) did a very interesting experiment with baits that were very similar in coloration as measured by reflectance spectra. They found apostatic selection as would be expected from figure 2 with C close to 1. It would be valuable to repeat this experiment with baits whose reflectance spectra differed in known ways from the background spectra and explore the parameter space of figure 2.

If there is anti-apostatic selection ($K < 0$) then the population will become monomorphic for the morph that is more cryptic. For intermediate C there will be an unstable equilibrium, with less restrictive conditions as K becomes more negative (figure 2). In natural populations this would always lead to monomorphism. This is also expected from the single-predator models of aposematic coloration (Fisher 1930; Greenwood 1984; Thompson 1984).

As long as the frequency-dependent relations of the two predators are approximately equal ($K_1 \approx K_2$) differences between the predators in perceived crypsis (C_1 and C_2) can be allowed for in the combined crypsis measure C. However, as soon as K_1 becomes very different from K_2, the equilibrium conditions become more complicated, and depend upon the relations between K_i and C_i. Let $K_1 \neq K_2$, the fitnesses in equations (11 *a*, *b*) are now:

$$W_A = C_1 P[1-K_1 f] + C_2(1-P)[1-K_2 f] \tag{15a}$$

and

$$W_a = P[1-K_1(1-f)] + (1-P)[1-K_2(1-f)]. \tag{15b}$$

The equilibrium is:

$$\hat{q}^2 = \frac{R-C+1}{R+K}, \tag{16}$$

where $C \equiv PC_1 + (1-P)C_2$ and $K \equiv PK_1 + (1-P)K_2$, as in (7) and (10), and $R \equiv PC_1K_1 + (1-P)C_2K_2$. R is a measure of the association between crypsis and frequency-dependence averaged over both predators. The equilibrium is stable and non-trivial if:

$$K > 1-C \quad \text{and} \quad R > C-1. \tag{17a, b}$$

In general R will be larger if the Cs and Ks for each predator are correlated. The covariance between the Cs and Ks is $\mathrm{cov}[C_i, K_i] = R - CK = P(1-P)(C_1-C_2)(K_1-K_2)$. Rearranging in terms of R, C and K, we obtain

$$R = \mathrm{cov}[C_i, K_i] + CK. \tag{18}$$

Substituting (18) into (17 *b*) the general conditions for stable non-trivial equilibria become

$$K > 1-C \quad \text{and} \quad K > 1-(1/C) - \mathrm{cov}[C_i, K_i]/C. \tag{19a, b}$$

Depending upon the relative values of the Ks, Cs and the covariance between each predator's C_i and K_i, zones of stability and instability can be large, small or non-existent. If the covariance is zero a stable equilibrium is only possible if there is apostatic selection ($K > 0$); this is identical to equation (14 *a*, *b*) (figure 2). If $\mathrm{cov}[C_i, K_i] > 0$, there can be a stable equilibrium with some anti-apostatic selection ($K < 0$) provided that the tendency to monomorphism for one morph due to $K < 0$ is balanced by an average crypsis favouring the other morph (figure 3). If $\mathrm{cov}[C_i, K_i] < 0$, a stable equilibrium is unlikely. The conditions for stability are less stringent for larger $\mathrm{cov}[C_i, K_i]$, a stronger association between crypsis and the strength of the frequency-dependence (19 *b*).

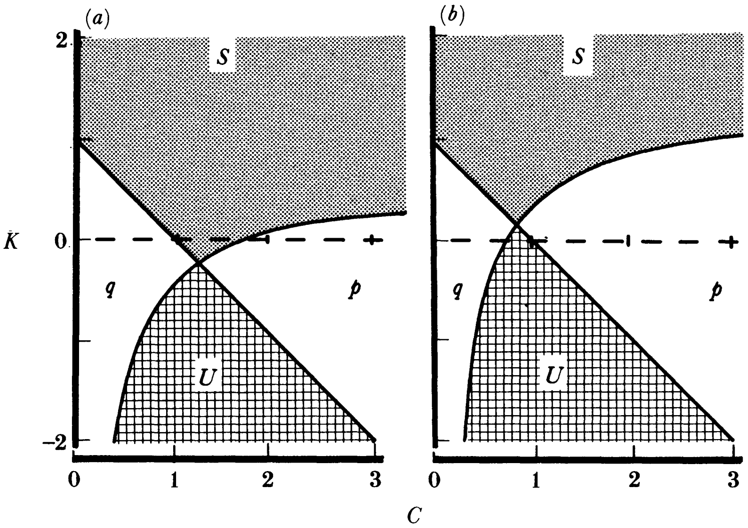

FIGURE 3. Conditions for spread or equilibrium with different strengths of frequency-dependent selection by each predator ($K_1 \neq K_2$) and a nonzero covariance between the crypsis and frequency-dependent parameters of each predator (cov $[C_i, K_i] \neq 0$). Lines and symbols as in figure 2, except: S, stable; U, unstable; q, q fixed; p, p fixed. (a) Arbitrary cov $[C_i, K_i] > 0$. Note how a stable equilibrium (shaded) is now possible with $K < 0$ (some anti-apostatic selection). (b) Arbitrary cov $[C_i, K_i] < 0$. A stable equilibrium is less likely for a given K and C, and requires a larger positive K.

Expressions (16), (17a, b) and (19a, b) can apply to n predators instead of two predators if we define $C \equiv \sum P_i C_i$, $K \equiv \sum P_i K_i$, and $R \equiv \sum P_i C_i K_i$, where P_i is the proportional risk due to predator i, and $\sum P_i = 1$. The results are similar in that it is the weighted average crypsis, frequency-dependence and covariance that determines the equilibrium or fixed allele. This model can also be modified to allow one morph to be palatable (Ks positive) and another morph is distasteful (Ks negative), as in Thompson's (1984) single-prey models. Then the conditions for stability and non-triviality depend upon a delicate balance between the different degrees of crypsis (C_is), the risks (P), strengths and signs of the frequency-dependence of the predators (K_is) and the association between crypsis and frequency-dependence (cov $[C_i, K_i] = R - CK$).

For most sets of parameters, but especially for $K_1 \neq K_2$ with $C_1 \neq C_2$, small changes in crypsis of one or more morphs can result in a transition between polymorphism and monomorphism, or the reverse, and so too can a small change in the proportionate risk of one of the two predators (P). Such changes may occur as a result of optimum foraging adjustments (Getty & Krebs 1985), seasonal shifts in other food taken by predators, and seasonal or daily changes in visual conditions or hunger. Immigration of new individual predators into an area may also affect the dynamics. If we allow the predator to evolve along with the prey, and allow it to evolve optimal foraging (Ps change), then the dynamics may be even more complex, and this has not been investigated.

To make matters more interesting, as the relative risk of predators changes in ecological or evolutionary time, the relative importance of different kinds of anti-predator defences changes. This may result in an increase in the efficiency of defence against one predator at the expense of a decreased efficiency against another (Pearson 1985). Because certain combinations of defences will work well against some predators at certain densities, but not at other densities or predators (Pearson 1985), transitions between polymorphism and monomorphism could be sudden, even for small shifts in the predator communities. We clearly need to know much more about the theoretical and empirical dynamics of multiple-prey–multiple-predator systems, and the vision and visual conditions of predators.

CONCLUSIONS

If predators exercise frequency-dependent selection on prey that vary in colour patterns, the prey may in some cases become monomorphic, and in other cases reach an equilibrium with more than one colour morph present within the foraging range of the predators. The outcome is a function of many different biological factors, some properties of the predators and some properties of the prey. Predator factors include requirements for optimal food choice, learning abilities, cognitive abilities, visual abilities, visual conditions during predation, diurnal and seasonal timing of predation, and the proportion of each predator and its risk to the prey. Prey factors include crypsis, choice of visual background and conditions and defences against the predators that operate after it is detected such as ability to run away, noxiousness, mechanical defence, distastefulness and lethality to the predators. The actual combination of these biological factors determines whether or not there is frequency-dependent selection, and whether or not it is apostatic or anti-apostatic. Thus even if frequency-dependent selection operates, it is no guarantee that it will maintain colour pattern polymorphisms. Depending upon the interaction between all of these factors, certain morphs may be actively maintained in some conditions and not in others, even with the same predators. More than one predator taxon will also affect stability, and only slight changes in conditions can cause a transition between polymorphism and monomorphism. Frequency-dependent selection is not a panacea for the explanation of variation in animal colour patterns, although it may be important in some systems.

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REFERENCES

Allen, J. A. & Anderson, K. P. 1984 Selection by passerine birds is anti-apostatic at high prey density. *Biol. J. Linn. Soc.* **23**, 237–246.

Archer, S. N., Endler, J. A., Lythgoe, J. N. & Partridge, J. C. 1987 Visual pigment polymorphism in the guppy, *Poecilia reticulata. Vision Res.* **27**, 1243–1252.

Arnason, E. 1978 Apostatic selection and kleptoparasitism in the Parasitic Jaeger. *Auk* **95**, 377–381.

Arnold, S. J. 1978 The evolution of a special class of modifiable behaviors in relation to environmental patterns. *Am. Nat.* **112**, 415–427.

Bobisud, L. E. & Potratz, C. J. 1976 One-trial versus multi-trial learning for a predator encountering a model-mimic system. *Am. Nat.* **110**, 121–128.

Bond, A. B. 1983 Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. *J. exp. Psychol.* **9**, 292–306.

Brakefield, P. M. 1985 Polymorphism, Müllerian mimicry, and interactions with thermal melanism in ladybirds and a soldier beetle: an hypothesis. *Biol. J. Linn. Soc.* **26**, 243–267.

Brower, L. P., Alcock, J. & Brower, J. V. Z. 1971 Avian feeding behaviour and the selective advantage of incipient mimicry. In *Ecological genetics and evolution* (ed. E. R. Creed), pp. 261–274. Oxford: Blackwell Scientific Publications.

Brown, K. S. Jr & Benson, W. W. 1974 Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid. Nymph.). *Biotropica* **6**, 205–228.

Bryan, J. E. 1972 Feeding history, parental stock, and food selection in rainbow trout. *Behaviour* **45**, 123–153.

Clarke, B. C. 1962 Balanced polymorphism and the diversity of sympatric species. In *Taxonomy and geography* (ed. D. Nichols), pp. 47–70. Oxford: Systematics Association.

Clarke, B. C. 1969 The evidence for apostatic selection. *Heredity* **24**, 347–353.

Clarke, B. C. & O'Donald, P. 1964 Frequency-dependent selection. *Heredity* **19**, 201–206.

Cook, L. M. 1983 Polymorphism in a mangrove snail in Papua New Guinea. *Biol. J. Linn. Soc.* **20**, 167–173.

Cook, L. M. 1986 Polymorphic snails on varied backgrounds. *Biol. J. Linn. Soc.* **29**, 89–99.

Cook, L. M. & Miller, P. 1977 Density-dependent selection on polymorphic prey – some data. *Am. Nat.* **111**, 594–598.

Cooper, J. M. 1984 Apostatic selection on prey that match the background. *Biol. J. Linn. Soc.* **23**, 221–228.

Coppinger, R. P. 1969 The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. I. Reactions of wild-caught adult blue jays to novel insects. *Behaviour* **45**, 45–60.

Coppinger, R. P. 1970 The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. II. Reaction of naive birds to novel insects. *Am. Nat.* **104**, 323–335.

Endler, J. A. 1978 A predator's view of animal color patterns. *Evol. Biol.* **11**, 319–364.

Endler, J. A. 1980 Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.

Endler, J. A. 1983 Natural and sexual selection on color patterns in poeciliid fishes. *Envir. Biol. Fishes.* **9**, 173–190.

Endler, J. A. 1984 Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**, 187–231.

Endler, J. A. 1986 Defense against predation. In *Predator–prey relationships, perspectives and approaches from the study of lower vertebrates* (ed. M. E. Feder & G. V. Lauder), pp. 109–134. University of Chicago Press.

Endler, J. A. 1987 Predation, light intensity, and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Anim. Behav.* **35**, 1376–1385.

Estabrook, G. F. & Jesperson, D. C. 1974 Strategy for a predator encountering a model-mimic system. *Am. Nat.* **108**, 443–457.

Fisher, R. A. 1930 *The genetical theory of natural selection.* London: Oxford University Press.

Gendron, R. P. 1986 Searching for cryptic prey: evidence for optimal search rates and the formation of search images in quail. *Anim. Behav.* **34**, 898–912.

Gendron, R. P. & Staddon, J. E. R. 1983 Searching for cryptic prey: the effect of search rate. *Am. Nat.* **121**, 172–186.

Getty, T. 1985 Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. *Am. Nat.* **125**, 239–256.

Getty, T. & Krebs, J. R. 1985 Lagging partial preferences for cryptic prey: a signal detection analysis of great tit foraging. *Am. Nat.* **125**, 39–60.

Gibson, D. O. 1980 The role of escape in mimicry and polymorphism: I. The response of captive birds to artificial prey. *Biol. J. Linn. Soc.* **14**, 201–214.

Gittleman, J. L. & Harvey, P. H. 1980 Why are distasteful prey not cryptic? *Nature, Lond.* **286**, 149–150.

Goodale, M. A. & Sneddon, I. 1977 The effect of distastefulness of the model on the predation of artificial Batesian mimics. *Anim. Behav.* **25**, 660–665.

Greenwood, J. J. D. 1969 Apostatic selection and population density. *Heredity* **24**, 157–161.

Greenwood, J. J. D. 1984 The functional basis of frequency-dependent selection. *Biol. J. Linn. Soc.* **23**, 177–199.

Greenwood, J. J. D. 1985 Frequency-dependent selection by seed predators. *Oikos* **44**, 195–210.

Guilford, T. 1985 Is kin selection involved in the evolution of warning coloration? *Oikos* **45**, 31–36.

Guilford, T. 1986 How do "warning colours" work? Conspicuousness may reduce recognition errors in experienced predators. *Anim. Behav.* **34**, 286–288.

Guilford, T. & Dawkins, M. S. 1987 Search images not proven: a reappraisal of recent evidence. *Anim. Behav.* **35**, 1838–1845.

Hailman, J. P. 1979 Environmental light and conspicuous colors. In *The behavioural significance of color* (ed. E. H. Burtt, Jr), pp. 289–354. New York: Garland STPM Press.

Harvey, P. H., Bull, J. J., Pemberton, M. & Paxton, R. J. 1982 The evolution of aposematic coloration in distasteful prey: a family model. *Am. Nat.* **119**, 710–719.

Harvey, P. H. & Paxton, R. J. 1981 The evolution of aposematic colouration. *Oikos* **37**, 391–396.

Hinton, H. E. 1976 Possible significance of the red patches of the female crab spider *Misumena vatia*. *J. Zool.* **180**, 35–39.

Horsley, D. T., Lynch, B. M., Greenwood, J. J. D., Hardman, B. & Mosely, S. 1979 Frequency-dependent selection by birds when the density of prey is high. *J. Anim. Ecol.* **48**, 483–490.

Hubbard, S. F., Cook, R. M., Glover, J. G. & Greenwood, J. J. D. 1982 Apostatic selection as an optimal foraging strategy. *J. Anim. Ecol.* **51**, 625–633.

Hughes, J. M. & Jones, M. P. 1985 Shell colour polymorphism in a mangrove snail, *Littorina* sp. (Prosobranchia: Littorinidae). *Biol. J. Linn. Soc.* **25**, 365–378.

Jacobs, G. H. & Neitz, J. 1987 Polymorphism of the middle wavelength cone in two species of South American monkeys: *Cebus apella* and *Callicebus moloch*. *Vision Res.* **27**, 1263–1268.

Landeau, L. & Terborgh, J. 1986 Oddity and the "confusion effect" in predation. *Anim. Behav.* **34**, 1372–1380.

Lawrence, E. S. & Allen, J. A. 1983 On the term "search image". *Oikos* **40**, 313–314.

Leimar, O., Enquist, M. & Sillén-Tullberg, B. 1986 Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *Am. Nat.* **128**, 469–490.

Lewontin, R. C. 1958 A general method for investigating the equilibrium of gene frequency in a population. *Genetics* **43**, 419–434.

Lythgoe, J. N. 1979 *The ecology of vision*. Oxford University Press.

Mallet, J. 1986 Hybrid zones of *Heliconius* butterflies in Panama and the stability and movement of warning colour clines. *Heredity* **56**, 191–202.

Mallet, J. & Barton, N. 1988 Strong natural selection in a warningly coloured butterfly. *Evolution*. (Submitted.)

Mallet, J. & Singer, M. C. 1987 Individual selection, kin selection and the shifting balance in the evolution of warning colours in butterflies. *Biol. J. Linn. Soc.* **32**, 337–350.

Maynard Smith, J. & Hoekstra, R. 1980 Polymorphism in a varied environment: how robust are the models? *Genet. Res.* **35**, 45–57.

McFarland, W. N. & Munz, F. W. 1975 The photic environment of clear tropical seas during the day. *Vision Res.* **15**, 1063–1070.

Neitz, J. & Jacobs, G. H. 1986 Polymorphism of the long-wavelength cone pigment in normal colour vision. *Nature, Lond.* **323**, 623–625.

Paulson, D. R. 1973 Predator polymorphism and apostatic selection. *Evolution* **27**, 269–277.

Pearson, D. L. 1985 The function of multiple anti-predator mechanisms in adult tiger beetles (Coleoptera: Cicindelidae). *Ecol. Ent.* **10**, 65–72.

Reid, D. G. 1987 Natural selection for apostasy and crypsis acting on the shell colour polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby) (Gastropoda: Littorinidae). *Biol. J. Linn. Soc.* **30**, 1–24.

Schlenoff, D. H. 1984 Novelty: a basis for generalization in prey selection. *Anim. Behav.* **32**, 919–921.

Sillén-Tullberg, B. 1985 Higher survival of an aposematic than of a cryptic form of a distasteful bug. *Oecologica* **67**, 411–415.

Sillén-Tullberg, B. & Bryant, E. H. 1983 The evolution of apostatic colouration in distasteful prey: an individual selection model. *Evolution* **37**, 993–1000.

Smith, J. N. M. 1974 The food searching behaviour of two European thrushes II: the adaptiveness of the search patterns. *Behaviour* **49**, 1–61.

Smith, S. M. 1975 Innate recognition of coral snake pattern by a possible avian predator. *Science, Wash.* **187**, 759–760.

Smith, S. M. 1977 Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature, Lond.* **265**, 535–536.

Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory*. Princeton University Press.

Thompson, V. 1984 Polymorphism under apostatic and aposematic selection. *Heredity* **53**, 677–686.

Turner, J. R. G. 1984 Mimicry: the palatability spectrum and its consequences. In *The biology of butterflies* (ed. R. I. Vane-Wright & P. R. Ackery), pp. 141–161. London: Academic Press.

Turner, J. R. G., Kearney, E. P. & Exton, L. S. 1984 Mimicry and the monte carlo predator: the palatability spectrum and the origins of mimicry. *Biol. J. Linn. Soc.* **23**, 247–268.

Vaughan, F. A. 1983 Startle responses of blue jays to visual stimuli presented during feeding. *Anim. Behav.* **31**, 385–396.

Wickler, W. 1968 *Mimicry in plants and animals*. New York: World University Library.

Wicklund, C. & Jarvi, T. 1982 Survival of distasteful insects after being attacked by naive birds: a reappraisal of the theory of aposematic colouration evolving through individual selection. *Evolution* **36**, 998–1002.

Willis, A. J., McEwan, J. W. T., Greenwood, J. J. D. & Elton, R. T. 1980 Food selection by chicks, effects of colour, density, and frequency of food types. *Anim. Behav.* **28**, 874–879.

Discussion

J. J. D. GREENWOOD (*Department of Biological Sciences, University of Dundee, U.K.*). Dr Endler remarks that it is possible to have frequency-dependent selection that is not, in itself, stabilizing. This is true: one form may be taken in excess at all frequencies even though the strength of selection may vary with frequency. I have referred to this as 'potentially apostatic' selection (Greenwood 1984). It is obviously important to distinguish it from cases that are truly apostatic, in that the direction of selection is different at the two ends of the frequency spectrum. This is difficult if there is strong frequency-independent selection as well as frequency-dependent, so that the switch in direction of selection occurs only when one of the forms is exceedingly rare. The statistical methods available are rather rough and ready and the problem is made especially difficult because the difference between the cases may only be apparent at extreme frequencies, at which there is huge sampling variance in the experimental results. Has Dr Endler any suggestions as to how one might distinguish the cases experimentally?

J. A. Endler. I completely agree with Dr Greenwood's comment that frequency-dependent and frequency-independent selection could be of sufficient relative magnitudes that the frequency-dependent portion would be nearly or actually ineffective. In terms of figures 2 and 3 this is equivalent to saying that the values of K and C for a particular species, subject to a particular local suite of predators, may be close to one of the boundary lines between stable equilibrium and selection for only one morph. Dr Greenwood raises the difficult practical problem of how to demonstrate and measure the frequency-dependent component (K) under these circumstances. Manley (1985) summarizes in detail the best statistical methods for estimating the form of a selection function. There is still the problem of sample sizes for doing this in an undisturbed natural population when C is quite different from 1.0. Perhaps one solution would be to attempt to measure C and K separately, by experimentation. Prepare baits to be exposed to the actual prey's natural predators on its natural backgrounds; the baits should have known crypsis values (measured as in Endler (1984)) and vary in crypsis value in such a way as to overlap the crypsis value of the actual prey. Experiments can be done in the same way as Allen and his colleagues (Allen, this symposium). Start with two equally cryptic (Endler 1984) colour patterns. Present them in, say, five different frequencies and work out the frequency-dependent fitness function, and replicate the experiment until the standard errors are as low as practical. Repeat the entire experiment by using two equally cryptic colour patterns that are more cryptic than the natural prey. Repeat the entire experiment again, with two equally cryptic colour patterns that are less cryptic than the natural prey. This will yield three fitness-frequency functions (which can be used to estimate K), with crypsis values more, equal to and less than the natural prey. Choose the portion of each curve (morph frequency) with the minimum standard error, and use this frequency to repeat the experiment yet again with two prey with different crypsis measures. Vary the relative crypsis to obtain an estimate of C, and then ask what part of the parameter space (figures 2 and 3) the population may be in. Is polymorphism expected with the estimated parameters (statistics)? It would be very interesting to do this kind of experiment using as a model a prey species that is monomorphic in some populations and polymorphic in others.

Reference

Manley, B. J. J. 1985 *The statistics of natural selection.* London: Chapman & Hall.