Evolutionary perspective

Perceptual processes and the maintenance of polymorphism through frequency-dependent predation

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Abstract. One of the key challenges of both ecology and evolutionary biology is to understand the mechanisms that maintain diversity. Negative frequency-dependent selection is a powerful mechanism for maintaining variation in the population as well as species diversity in the community. There are a number of studies showing that this type of selection, where individuals of a rare type (i.e. a rare morph or a rare species) experience higher survival than those of more common type(s). However, it is still not clear how frequency-dependent selection operates. Search image formation has been invoked as a possible, proximate explanation. Although the conceptual link between search image and frequency-dependent predation is often assumed in ecological and evolutionary studies, a review of the literature reveals a paucity of evidence demonstrating the occurrence of *both* in a natural predator-prey system. Advances in the field of psychology strongly support the existence of search image, yet these findings are not fully recognized in the realm of ecology and evolutionary biology, in part, we feel because of confusion and inconsistencies in terminology. Here we try to simplify the language, clarify the advances in the study of frequency-dependent predation and search image, and suggest avenues for future research. We feel that the investigations of both proximate (perceptual mechanisms) and ultimate (pattern of predation) processes are necessary to fully understand the importance of individual behavioural processes for mediating evolutionary and ecological diversity.

Key words: apostatic selection, diversity, frequency-dependent selection, polymorphism, predation, search image, switching, variation

Introduction

One of the paradoxes of evolutionary biology is the persistence of high levels of genetic variation, despite the eroding effects of natural selection and genetic drift (Lewontin, 1974). It has been demonstrated, theoretically, that there are several evolutionary mechanisms that are capable of maintaining high levels of polymorphism (Charlesworth, 1987; Barton and Turelli, 1989). A particularly powerful mechanism is negative frequency-dependent selection, where the relative fitness of a genotype declines as its relative abundance in a population

increases. This type of selection is potentially capable of maintaining large numbers of alleles at individual loci (Wright, 1948; Li, 1962; Clarke and O'Donald, 1964; Ayala and Campbell, 1974). Here we focus on one particular form of negative frequency-dependent selection (i.e. frequency-dependent predation) and the perceptual mechanisms that may underlie this form of selection. This area of study has received considerable attention from researchers from a range of fields in evolution, ecology and psychology. We review some of the major advances in these areas of study and evaluate their importance for maintaining genetic polymorphism in natural populations.

Frequency-dependent predation

One commonly documented form of negative frequency-dependent selection occurs when predators consume disproportionately more of a particular prey type when it is common and less of that prey type when it is rare (e.g. Cain and Sheppard, 1954; Haldane, 1955; May, 1977; Thompson, 1984; Allen, 1988a; Endler, 1988; Bond and Kamil, 1998, 2002). Poulton (1884) was probably the first author to recognize the importance of frequency-dependent predation; he hypothesized that colour polymorphism in geometrid moth larvae (*Cyclophora* spp.) was actively maintained by selection imposed by predators (Poulton, 1884; Allen and Clarke, 1984). Clarke (1962a, b) provided early evidence of the role of frequency-dependent predation in maintaining polymorphism in wild populations of land snails (*Cepaea* spp.). He found that the relative abundance of a particular morph in its habitat was highly correlated with how cryptic the morph was in that habitat, but noted that even non-cryptic morphs could persist within a population at low frequencies. Clarke (1962a, b) hypothesized that frequency-dependent predation, which he referred to as apostatic selection (see Appendix 1 for explanation), was responsible for maintaining this polymorphism (but also see Jones *et al.*, 1977; Cook, 1998).

Although many subsequent studies have invoked frequency-dependent predation as a possible explanation for the persistence of colour pattern polymorphisms to natural populations (e.g. Moment, 1962; Owen and Wiegert, 1962; Endler, 1980; Owen and Whiteley, 1986; Gillespie and Tabashnik, 1990; Whiteley *et al.*, 1997; Gillespie and Oxford, 1998), none of these studies have provided experimental evidence of frequency-dependent predation. Demonstrating frequency dependent predation typically requires the use of selective predation experiments in which alternative prey types are presented in varying relative frequencies. One of the earliest experiments providing evidence for frequency-dependent predation came from laboratory studies of predation by a fish, the Rudd (*Leuciscus erythropthalamus*), on an aquatic insect, the water boatman (*Arctocorisa distincta*) (Popham, 1941). Popham

found that prey-types 'occurring in the greatest numbers were destroyed relatively faster than the others and not in direct proportion to their numbers' (P. 149). Since then, numerous selective predation experiments have demonstrated frequency-dependent predation on polymorphic prey (e.g. Clarke, 1962a, b; Croze, 1970; Allen, 1972; Cook and Miller, 1976; Cooper, 1984; Reid, 1987; Allen et al., 1998; Bond and Kamil, 1998, 2002), prompting the development of several explicit models for the analysis of such experiments (e.g. Manly, 1972, 1973, 1974; Manly et al., 1972; Greenwood and Elton, 1979; Greenwood, 1984; Weale and Allen, 1989).

In addition to its importance for the maintenance of intraspecific variation, frequency-dependent predation may have implications for maintaining species diversity at the community level. Ecologists recognized that when the abundance of a particular food source becomes low, predators tend to 'switch' from that source to another (e.g. Holling, 1959; Murdoch, 1969; Murdoch et al., 1975; Hughes and Croy, 1993). 'Switching' (see Appendix 1) is believed to be capable of promoting the coexistence of competing prey species (Murdoch and Oaten, 1975; Roughgarden and Feldman, 1975; May, 1977), at least under certain conditions (see Holt, 1984; Abrams, 1999).

Search image hypothesis

Despite the number of studies presenting evidence of frequency-dependent predation, a clear proximate mechanism for this pattern of predation has been difficult to demonstrate. Many have suggested that behavioural processes mediated at the level of individual predators are responsible for generating frequency-dependent predation (e.g. Moment, 1962; Clarke, 1962a; Bond, 1983; Lawrence, 1985; Gendron, 1986; Allen, 1988a, b; Endler, 1988; Gillespie and Tabashnik, 1990; Dukas and Ellner, 1993; Dukas and Kamil, 2001). One of the most widely investigated mechanisms is search image (formation) (e.g. Dawkins, 1971a, b; Pietrewicz and Kamil, 1977, 1979; Bond, 1983; Lawrence, 1985; Gendron, 1986; Bond and Kamil, 1998, 2002). This mechanism was first proposed by Tinbergen (1960), in his study of predation by great tits (*Parus major*) on the larvae of various insect species. Comparisons between the numbers of larvae captured and their relative abundance revealed that the birds had captured disproportionately more of the common prey while generally overlooking the rare prey. Tinbergen proposed that this effect was the result of perceptual processes occurring in the predator, referred to as 'adopting a search image', whereby prior experience with a certain prey-type facilitates the detection of the same prey-type in subsequent encounters. More simply put, the search image hypothesis postulates that predators are better at

detecting familiar prey, because they have 'learned to see them' (Guilford and Dawkins, 1987).

Although the term 'search image' is used by psychologists to refer to one form of stimulus-selective attention (Dukas, 2002), the term has often been misused, especially in ecological and evolutionary studies (see Appendix 2). Search image is defined as a *perceptual* change in the ability of a predator to detect familiar, *cryptic* prey (Tinbergen, 1960; Dawkins, 1971a; Lawrence and Allen, 1983). Dukas (2002) suggests a more precise definition of search image: 'a selective search for a particular cryptic prey type, which involves an increased probability of detecting that prey type and a reduced probability of detecting other distinct prey types' (p.1542). It is believed that search image is the result of constraints on attention and information processing when trying to detect cryptic prey (Dawkins, 1971b; Bond, 1983; Dukas and Ellner, 1993; Dukas, 2002). Foragers must 'divide attention' when engaging in multiple tasks simultaneously, resulting in decreased foraging efficiency (Dukas and Real, 1993). Therefore, temporarily specializing in only one foraging task (i.e. one prey-type) at a time results in greater foraging efficiency; thus, search image formation can be considered to be adaptive, allowing a predator to forage more efficiently when a particular prey-type is locally abundant (Greenwood, 1985; Dukas and Kamil, 2001).

There is substantial neurophysiological evidence of the finite nature of attention. Several studies have demonstrated that increased neuron activity associated with a specific task results in decreased neuron activity in other parts of the brain (e.g. Rees *et al.*, 1997; de Fockert *et al.*, 2001; Spinks *et al.*, 2004; also see Dukas, 2002 and references therein). This trade-off at the neural level further supports the notion that limited attention reflects constraints on information processing.

Limited attention in predators could ultimately promote maintenance of infra-specific (and presumably, inter-specific) variation in prey, as there is evidence that polymorphic prey are overall more difficult to detect than monomorphic prey (Glanville and Allen, 1997). For similar reasons, constraints on information processing have led some researchers to suggest that perceptual mechanisms in foraging insect pollinators may also explain flower constancy (Goulson, 2000) and even flower corolla polymorphism (Smithson and MacNair, 1997; Gigord *et al.*, 2001; Castillo *et al.*, 2002). Search image in an herbivorous insect has also been proposed as a proximate explanation for the divergence in leaf shape among host plants (Rausher, 1978). The effects of search image are believed to be only temporary (Dawkins, 1971b; Lawrence and Allen, 1983; Langley *et al.*, 1996; Plaisted, 1997), and its effects are evident only when prey are cryptic (Dawkins, 1971a; Reid and Shettleworth, 1992; Langley *et al.*, 1996; Kono *et al.*, 1998).

The search image controversy

Marshalling evidence to support the hypothesis that search image formation causes negative frequency-dependent selection has, however, been controversial. Most studies have attempted to demonstrate search image through feeding trials in which predators were presented with different sequences of prey items. A series of classic studies by Pietrewicz and Kamil (1977, 1979) were among the first to explicitly test for search image. They employed operant techniques in which blue jays (*Cyanocitta cristata*) were rewarded for detecting (i.e. pecking at) photographic images of cryptic moths resting on various backgrounds. These 'prey' were presented to blue jays in sequences of photographic slides, in two experimental treatments: 'run' sequences (containing only one prey-type) vs. 'mixed' sequences (containing two types, in equal proportions). As predicted by the search image hypothesis, prey detection rates in the mixed sequence were significantly lower than in the run sequence. The discrepancy in detection rates was interpreted as being the result of perceptual interference during the mixed sequences, because the predators had to deal with two possible prey-types, instead of just one. However, Guilford and Dawkins (1987) reinterpreted the 'evidence' of search image (i.e. Pietrewicz and Kamil, 1977, 1979; also Dawkins, 1971a, b; Bond, 1983; Lawrence, 1985; Gendron, 1986) and postulated an alternative hypothesis: the search rate hypothesis. They argued that predators can improve the probability of detecting cryptic prey by simply decreasing their rate of visual search, essentially 'searching longer' when scanning a potential patch (see also Gendron and Staddon, 1983). Although the search rate hypothesis does not predict any perceptual interference associated with multiple prey, it can explain why predators exhibit a decreased foraging rate when presented with multiple morphs of unequal degrees of crypsis; when alternative prey are not equally cryptic, the lower efficiency when foraging upon mixed prey merely reflects the increased time spent searching for the more cryptic of the two prey types. Since the alternative prey used in Pietrewicz and Kamil's (1979) experiment were not equally cryptic, the search rate hypothesis could not be ruled out (Guilford and Dawkins, 1987). The distinction between the two hypotheses is important because search rate does not cause frequency-dependent predation, and it therefore cannot explain the maintenance of polymorphism (Guilford and Dawkins, 1987).

Subsequent studies aiming to distinguish between search image and the search rate hypothesis (e.g. Reid and Shettleworth, 1992; Plaisted and Mackintosh, 1995) examined foraging performance in studies similar to Pietrewicz and Kamil (1979), but they used equally cryptic artificial prey. The results of these studies were consistent with Pietrewicz and Kamil's (1979) studies, supporting the search image hypothesis over search rate. Plaisted (1997), however, offered a novel explanation for the results of Pietrewicz and Kamil (1979), and

Plaisted and Mackintosh (1995). She argued that their results were confounded by differences between run and mixed treatments, in the absolute rate of presentation of prey types. Because the inter-target interval (i.e. the duration between successive presentations of prey items, regardless of which type) was held constant in both treatments, the inter-stimulus interval (i.e. the duration between the presentation of a specific prey type) was necessarily longer for the mixed than the run treatments.

She reasoned that the poor performance (i.e. decreased foraging success) on mixed treatments was also consistent with theories of short-term memory decay. These results would be expected if foragers are able to maintain multiple search images but with effects that deteriorate over time. To test this hypothesis, Plaisted (1997) conducted a series of experiments in which inter-stimulus interval was carefully controlled. As she predicted, performance improved on both mixed and run treatments when the inter-stimulus interval was short but, when the inter-stimulus was long, performance on mixed treatments was poor. It should be noted, however, that although Plaisted's (1997) alternative explanation is consistent with the data, it does not refute the search image hypothesis; rather, it is an extension of search image, highlighting the temporary nature of its effects.

Criticisms and considerations for future research

Despite its intuitive appeal, assuming causal links between search image, frequency-dependent predation and polymorphism is problematic. Although search image may result in frequency-dependent predation, which in turn can maintain prey polymorphism, the reasoning does not hold in the reverse direction; prey polymorphism is not necessarily indicative of frequency-dependent predation nor of search image.

Although search image is supported by numerous laboratory studies, these studies were performed in only a handful of vertebrate (avian species of) predators (e.g. Dawkins, 1971a, b; Pietrewicz and Kamil, 1979; Blough, 1991, 1992; Bond and Riley, 1991; Reid and Shettleworth, 1992; Blough and Lacourse, 1994; Plaisted and Mackintosh, 1995; Langley, 1996; Bond and Kamil, 1998, 2002). It is unclear whether search image is common across vertebrate and invertebrate taxa. Also, it is unknown whether predators commonly employ search images in the wild. The use of search image by predators may be contingent on the visual background (i.e. microhabitat) against which prey are viewed (Kono et al., 1998). If prey is conspicuous, predators may not need to employ search image at all (Dawkins, 1971a). Even when a morph is cryptic against a particular substrate, the same morph will seldom be equally cryptic against a different substrate. This trade-off in crypsis across micro-

habitats mean that search image may have relevance in only a limited subset of search tasks and frequency-dependent selection could be weak or non-existent. Furthermore, the visual heterogeneity of habitat can have a strong effect upon whether prey colouration evolves to maximize crypsis in a single background or to maximize crypsis in all backgrounds (Endler, 1978; Merilaita *et al.*, 1999, 2001). Habitat heterogeneity can therefore influence the form of selection on prey colouration and ultimately determine whether polymorphism is maintained.

The importance of search image in nature may also be dependent upon how frequently predators encounter specific prey types. Most experimental demonstrations of search image involved presentation of prey at relatively rapid rates (e.g. Pietrewicz and Kamil, 1979; Bond, 1983; Blough, 1991; Reid and Shettleworth, 1992; Plaisted and Mackintosh, 1995; Plaisted, 1997; Bond and Kamil, 1998). In these studies, the time elapsed between presentations typically ranged from several seconds to about a minute and a half. Given the short-term nature of its effects (e.g. Dawkins, 1971b; Langley *et al.*, 1996; Plaisted, 1997), search image may have limited importance in the wild if predators (under natural conditions) encounter prey at relatively low rates (i.e. when prey density is low). Theoretical and experimental studies have demonstrated that prey density and/or spatial distribution has profound effects on frequency-dependent food selection by predators (e.g. Greenwood, 1969; Cook and Miller, 1972; Harvey *et al.*, 1974; Horsley *et al.*, 1979; Willis *et al.*, 1980; Allen *et al.*, 1998; Shigemiya, 2004). For example, at extremely high density or when prey is aggregated, the direction of frequency-dependent predation may be reversed–rare morphs suffer heavier predation (e.g. Willis *et al.*, 1980; Horsley *et al.*, 1979; Greenwood, 1985; but see also Greenwood *et al.*, 1989; Weale *et al.*, 2000).

There is also a potential problem with predicting patterns of selection by an entire population of predators, solely from studies of the behaviour of individuals. Search image formation is a mechanism occurring at the individual-level; however, variation between individual predators can have complicated, sometimes unexpected, population-level consequences. For example, when predator preferences vary, the net effect of population-level predation can be positive frequency-dependent (i.e. favour common forms) despite individual predators foraging in a negative frequency-dependent manner (see Sherratt and MacDougall, 1995. Thus, unless population-level patterns of predation are known (i.e. inferred from selective predation experiments performed in the field), the relative importance of search image for maintaining prey polymorphism in nature remains unclear.

A potential problem with some of these studies is that they employed different prey species as alternative prey. Optimal foraging theory predicts changes in prey consumption in a manner that maximizes net energetic gain

(Charnov, 1976) and that diet choices should depend on a number of factors related to 'profitability' (*sensu* Royama, 1970; Curio, 1976). Undoubtedly different prey species have different energetic values, handling times, anti-predator behaviours and microhabitat use–all of which should affect the relative profitability of prey and the subsequent foraging *decisions* of predators. Failure to exclude differences among such factors confounds any study designed to address only the *perceptual* mechanisms contributing to frequency-dependent predation (Appendix 2). On the other hand, studies attempting to control for these confounding factors have employed artificial prey (e.g. dyed pastry, painted seeds) under artificial conditions and, hence, lack biological realism (Allen, 1989).

One avenue for resolving this problem lies in the use of prey species that naturally exhibit polymorphism. In some species, alternative phenotypes occur which, other than colouration, exhibit few obvious morphological or behavioural differences (e.g. periwinkles *Littorina* spp.; moths *Catocala* spp.; *Biston betularia*; spittlebug *Philaenus spumarius*; guppy *Poecilia reticulata*). Use of such morphs as alternative prey should provide experimental control without compromising biological realism. More importantly, experiments using polymorphic species has direct relevance for studies attempting to explain the maintenance of polymorphism. To date, however, there are very few (e.g. Reid, 1987; Jormalainen *et al.*, 1995) experimental demonstrations of frequency-dependent predation that have employed natural, polymorphic prey, and those did not address the proximate mechanism resulting in frequency-dependent predation.

Granted, using live prey in predation experiments can be difficult and it is no wonder why most studies have employed artificial prey. However, some clever alternatives have been devised to test frequency-dependent predation while avoiding the problems of using live prey. For example, Bond and Kamil (1998, 2002) conducted a series of studies of predation by blue jays (*Cyanocitta cristata*) on virtual populations of computer-generated (from digital images of *Catocala* spp.) moths. They demonstrated that visual predation by *C. cristata* promoted (Bond and Kamil, 2002) and maintained (Bond and Kamil, 1998, 2002) the phenotypic diversity of prey. These studies are particularly exciting because they are the first to demonstrate the numerical (i.e. changes in absolute abundance), as well as evolutionary (i.e. changes in relative morph frequencies), response of prey populations to selective predation through search image. To date, these studies provide the best evidence that search image is capable of maintaining prey polymorphism. To our knowledge, however, there is no evidence (i.e. field data) that blue jays forage in a frequency-dependent manner under natural conditions. That is, the studies clearly demonstrate that frequency-dependent predation resulting from search image *can* maintain prey polymorphism, but do not prove that these mechanisms *are* the processes

responsible for the maintenance of the polymorphism observed in *Catocala* moths. We are not aware of any studies examining alternative mechanisms that could be maintaining *Catocala* polymorphism.

Although there is compelling evidence for either search image or frequency-dependent predation in a number of systems, evidence of the occurrence of *both* in a naturally occurring predator–prey system is currently lacking; consequently, the importance of search image for maintaining prey polymorphisms in nature remains unclear. We feel that, in order to adequately examine this problem, future studies must include the following considerations. First, prey used in selective predation experiments should reflect variation that is realistic (i.e. drawn from a naturally occurring range of phenotypes). Second, the study system should reflect a natural predator–prey system, in which predators are believed to impose significant selection on the prey phenotype (e.g. colour pattern). Third, studies (ideally, in both laboratory and field) should investigate both proximate (i.e. perceptual) and ultimate (i.e. pattern of predation) processes, to capture the effects of individual behaviour, as well as population-level effects.

There is also the potential for comparative studies to contribute to the understanding of the evolution of polymorphism. A comparative approach has been employed in studies of cryptic (e.g. Whitely *et al.* 1997), mimetic (e.g. Vane-Wright *et al.*, 1975) and plumage polymorphisms in predatory birds (e.g. Fowlie and Kruger, 2003; Galeotti *et al.*, 2003). It is possible that search image and frequency-dependent predation maintain polymorphism only under certain ecological conditions (e.g. depending on density or habitat), which might be reflected in inter- or intra-population variation in levels of polymorphism. Although even controlled comparisons (e.g. phylogenetically independent contrasts) have limitations for inferring causation, patterns of correlations (or correspondence) between polymorphism and ecological variables could prove useful.

In light of these considerations, the guppy (*Poecilia reticulata*) is an excellent candidate system for studies of frequency-dependent predation, its behavioural basis (i.e. proximate cause) and its importance for maintaining colour pattern polymorphism. Guppies exhibit remarkably high levels of colour pattern polymorphism in nature, and the genetic basis of this variation is relatively simple and well understood (Winge, 1922; Winge and Ditlevsen, 1947; Houde, 1992). Predation by the cichlid *Crenicichla alta*, a visual predator, is believed to impose strong natural selection on various aspects of colour pattern in *P. reticulata* (Endler, 1980, 1983, 1995). Furthermore, several authors have invoked negative frequency-dependent selection, through predation (Endler, 1980), sexual selection (Farr, 1977; Hughes *et al.*, 1999), or some combination of both (Endler, 1988), as a possible explanation for the persistence of polymorphism in this species. Because *P. reticulata* easily adapts to

laboratory conditions and because colour pattern (in many populations) exhibits strong Y-linkage (Houde, 1992; Winge, 1922), it is possible to rear large numbers of alternative prey 'morphs' for predation experiments. In addition, the ecology of *P. reticulata* is conducive to release-recapture studies (Reznick *et al.*, 1996, 1997, 2001), making it relatively easy to conduct studies of frequency-dependent predation in both field and laboratory conditions.

It is also well documented that guppy populations exhibit differences in life history and morphology, corresponding to ecological differences including predation pressure and habitat (Endler, 1995; Rodd and Reznick, 1997; Reznick *et al.*, 2001; Grether *et al.*, 2001). Geographical and historical factors contributing to the genetic divergence among populations is also relatively well understood (Carvalho *et al.*, 1991; Fajen and Breden, 1992), which would aid in comparative analyses of the association between levels of polymorphism and various ecological factors. Previously, comparative studies of this nature were not possible, as indices for objectively quantifying and comparing complex colour patterns (like in guppies) were unavailable. Recently, however, Endler and Mielke (2005) have devised a statistical method that can be used to measure levels of colour polymorphism (i.e. dissimilarity) across populations (Endler, pers. comm.).

Investigating search image using species with non-avian predators, like guppies, may prove challenging, given the traditional methods of assaying the performance of predators in operant search tasks (e.g. pecking at projected targets on computer screens; but for an alternative method, see Morgan and Brown, 1996). Though these techniques have typically been restricted to domesticated birds, they may be applicable to *C. alta* (the predator), as various fish species have been shown to respond well to operant conditioning (e.g. Thompson, 1966; Gee *et al.*, 1994; Sevenster *et al.*, 1995; Parkyn *et al.*, 2003). Numerous studies have also successfully employed video equipment as stimuli for fish behaviour studies (reviewed in Rowland, 1999; see also Kunzler and Bakker, 2001; Morris *et al.*, 2003). Meeting various technical requirements (e.g. automated reward dispensers) may pose challenges but there already exist some mechanical devices (e.g. Chase and Hill, 1999) that could be modified for experiments on (visual) detection of prey. Taken together with experimental demonstrations of frequency-dependent predation and observed levels of guppy polymorphism in nature, evidence of search image would provide strong support for the notion that individual predator behaviour can maintain polymorphism.

Clearly, search image and frequency-dependent predation have potentially important ecological and evolutionary effects, but it is still unclear whether they are general phenomena in natural systems, and whether their occurrence is taxonomically widespread (see Sheratt and Harvey, 1993, for a review of frequency-dependent predation in arthropods). Future research examining the

links between polymorphism and predator behaviour should consider the use of a natural predator–(polymorphic) prey system. Framed in a biologically relevant context, combining studies of both proximate and ultimate causes can be very powerful for understanding the importance of individual perceptual processes for mediating evolutionary and ecological patterns of diversity.

Acknowledgements

Appendix 1. Synonyms of frequency-dependent predation

Evolutionary biologists have used several terms to refer to selective predation where predators consume disproportionately more of a particular prey type when it is common and disproportionately less of that prey type when it is rare. Clarke (1962a) referred to this type of selection as *apostatic*, as it confers an advantage to 'phenotypes that stand out from the norm' (p. 59). This term has since been adopted by many authors and is typically used in reference to the maintenance of intra-specific variation (polymorphism), though in its original context, it was also considered important in inter-specific variation (see below). Moment (1962) independently coined *reflexive selection* to refer to selection for 'variation *per se*' (p. 263), suggesting that polymorphism itself is adaptive. Although reflexive selection is similar to apostatic selection in that it predicts negative frequency dependent selection (and indeed, some consider the two synonymous; Allen, 1988b), there are some subtle differences in their meanings. Apostatic selection was initially coined to explain the dissimilarity of closely related species occurring in sympatry (Clarke, 1962a, b.) while reflexive selection was conceived to explain the occurrence of massive discontinuous variation within a species (Moment, 1962); Owen and Whitely (1986, 1989) suggest that the key difference between these terms lies in that apostatic selection is selection for contrasts between alternative types (morphs) while reflexive selection represents selection for variation itself. According to their definition, apostatic polymorphisms would be characterized by morphs each occurring at relatively high frequencies while reflexive polymorphisms would be evident as

massive diversity in which each morph is virtually unique (and thus, each occurring at low frequency).

Population ecologists use the term *switching* (Murdoch, 1969) to describe the tendency of predators to feed most heavily upon the most abundant species until this particular species declines in number, upon which, the predator 'switches the greater proportion of its attacks' to another, more abundant prey (p. 335). Although this term is used when referring to predation on different prey species, it is analogous to apostatic and/or reflexive selection (May, 1977). Switching is usually characterized by a sigmoid (i.e. type III, Holling, 1959) functional response and is generally considered to be capable of promoting the coexistence of competing prey species (Murdoch and Oaten, 1975; Rough-garden and Feldman, 1975; May, 1977).

Investigations of the behavioural mechanisms involved in the detection of prey have also demonstrated the effects of prey abundance on foraging patterns. Bond (1983) used the term *matching selection* to describe predation that exhibits a 'bias in favour of more frequent food types' (p. 292). Although this term was used to describe the pattern resulting from foraging tasks by individual predators, it essentially describes the same process of frequency-dependent predation, as defined by ecologists and evolutionary biologists.

Appendix 2. Distinguishing search image from other behavioural mechanisms promoting polymorphism

Search image clearly refers to a perceptual mechanism and should not be confused with other predator–mediated processes related to prior experience [e.g. altered search tactics, improvements in handling time, or preference/ aversion to a particular type of prey (Dawkins, 1971a; Krebs, 1973)] or to diet choices as predicted by optimal foraging theory (Charnov, 1976; Pyke *et al.*, 1977). It is also useful to distinguish search image from the avoidance of novel prey. There is evidence that predators exhibit an innate aversion towards unfamiliar prey (e.g. Coppinger, 1969, 1970; Marples *et al.*, 1998). Although neophobia (or dietary conservatism) may have important implications for colour pattern evolution – especially for aposematism (e.g. Mappes and Alatalo, 1997; Lindstrom *et al.*, 2001; Thomas *et al.*, 2003) – this mechanism is clearly not the result of selective attention and making this distinction is important for experimental tests of search image (Guilford and Dawkins, 1987). Nor is search image the result of failure to recognize a particular stimulus as valid prey (i.e. when prey is presumably detected but the predator presumably has not learned that it is palatable). Although predator psychology is considered important for the evolutionary dynamics of mimicry – including

the maintenance of mimetic polymorphisms (reviewed in Joron and Mallett, 1998; Mallett and Joron, 1999) – the behavioural mechanisms involved are attributed to learning and forgetting rather than to selective attention (MacDougall and Dawkins, 1998).

The effects of unfamiliarity and novelty have also been invoked to explain polymorphism in predators, as opposed to prey. Paulson (1973) attributed ventral plumage polymorphism in birds of prey to frequency-dependent selection favouring rare variants, as prey would not yet have learned to recognize the birds as a threat. This concept of prey learning to avoid specific phenotypes was later formalized as the 'avoidance image' hypothesis (Rohwer, 1983).

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