Search Image-driven Apostatic Selection and the Evolution of Phenotypic Polymorphism

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Understanding the mechanisms which actively maintain phenotypic variation in natural populations is an important consideration in evolutionary biology. Many cryptic prey species which rely upon avoiding visual detection by predators are also highly polymorphic, seemingly contradicting our expectation that selection would drive such a population towards a single, optimally concealed phenotype. When predators hunt for concealed prey in visually complex environments, they may filter what they see using a 'search image', consisting of the recalled phenotypic characters of previously encountered prey items. The use of search images can extend to phenotypically distinct morphs belonging to the same species, and in order to optimise a predator's foraging efficiency, they are more likely to be formed and retained for the most commonly encountered prey morphs. Hypothetically, common intraspecific colour morphs will therefore be subject to nonrandom and disproportionately high levels of predation, favouring the evolution of phenotypic diversity in otherwise cryptic prey species. A large but patchy, complex and often disconnected literature has developed which, although generally supportive of this mechanism, is far from conclusive.

Colouration, Perception and Deception

The colours of animals and plants are undoubtedly one of the most striking aspects of their phenotype, and their origins and purposes have long been the subject of speculation. This is perhaps not surprising since even the layman, with no technical biological training, cannot help but be intrigued by the meticulous resemblances of stick and leaf insects, or a peacock's cumbersome, ostentatious plumage. The functional bases of these remarkable displays are almost as diverse as their manifestations (Poulton, 1890; Beddard, 1892; Thayer, 1909; Cott, 1940; Fogden and Fogden, 1974; Owen, 1980). Colours may, for instance, serve a strictly physiological function such as we see in the increased tendency towards a general darkening of pigmentation in animal species and populations inhabiting northern latitudes (Kettlewell, 1973). This is thought to result from the physical properties of the colour itself, for darker colours both absorb and radiate heat more quickly, allowing ectotherms, which derive their heat from external sources, to warm up and become active more quickly in colder climates (Clusella Trullas *et al*., 2007). Colouration can also serve as a visual signal to other organisms, in both interspecific (e.g. warning colouration and mimicry) and intraspecific interactions (e.g. social signals such as threat and courtship displays) (reviewed in Cott (1940)). Such uses of colouration are distinct from physiological functions in that they explicitly involve the perception of another organism – that is, both the optical and neurological mechanisms employed for colour vision.

Colour is, fundamentally, a perception which results from the differential absorption and reflection of different wavelengths of electromagnetic radiation. Those wavelengths which are reflected by a material stimulate photoreceptor cells within an organism and give it its ascribed colour. Colour is not precisely an inherent property of an object, nor of electromagnetic radiation itself, but is rather a subjective experience of the observer, and how the visual system perceives the radiation captured by the senses. In this respect, colours are by their nature signals – they are a representation of the physical and chemical nature of the world as illustrated by its interaction with electromagnetic radiation. The visual systems of different animal species vary in their

specialisation and sensitivity to detecting different regions of the spectrum suitable to their own particular way of existence (selected examples given in Kelber *et al*. (2003)). It is thought that in primates, for example, an ability to perceive a range of colours which are not visible to other mammals has evolved, at least in part, to allow specialised food selection and increased predator detection (Carvalho *et al*., 2017). **See also: Colour Vision**

One prominent way in which colouration is utilised as an inter-specific signal is crypsis or cryptic colouration, generally referred to as camouflage. Typically we think of this as a means by which potential prey might conceal themselves from their respective predators, but it may equally be found among predators to avoid detection by their target prey. Poulton (1890), who first considered systematically the visual functions of animal coloura-tion, showed that cryptic colouration might be achieved either through a deceptive resemblance to a specific object in the environment (e.g. leaf mimicry in katydids or the stone-mimicking pebble plants *Lithops*) or much more commonly by simply 'harmonising with the general effect of the surroundings' so as to pass unnoticed (p. 20) (e.g. the contrasting summer and winter coats/plumage of many mammal and bird species). An organism's surroundings will of necessity change through space and time, and so selection for cryptic colouration will tend to drive an organism towards resembling the statistical average of the background environment against which it is most often viewed by the organisms it is seeking to deceive (Endler, 1978). When, where and by whom an organism is viewed determines the selective pressures acting upon its colouration. **See also: Mimicry**

Cryptic prey animals are adapted not simply to match their average environment, but that environment *as perceived* by their specific predators. Crypsis is therefore as much an adaptation to the visual systems of the respective perceiving organisms as it is to the environment against which the cryptic animal is perceived. In this article I consider how, in addition to highly effective cryptic resemblances, the visual systems and perceptual behaviours of other organisms also have the potential to select for a proliferation of phenotypic diversity. Since its introduction the concept of search images has been implicated in the evolution of colouration in many species, and a surprisingly broad literature has developed on the subject, much of which is not without its problems. Search images lie at the root of a compelling and elegant selective mechanism which has been invoked to explain puzzling instances of extensive phenotypic variation. I make no pretence herein to conduct a complete review of the literature on this mechanism – to do so would require many times the space. Instead, I trace the development of the idea, summarise the available evidence and consider the more notable criticisms. In presenting this survey of the topic, my hope is to clearly paint a picture of this mechanism and our understanding of it, forming a solid basis from which renewed interest might arise.

The Paradox of Cryptic Polymorphism

Through the action of natural selection we would expect that, in a stable environment, a prey population relying upon the avoidance of detection by predators would be driven towards a phenotypic optimum, such that a given individual's cryptic resemblance to its average background would be maximised. Paradoxically, however, there are a great many species which possess every indication of being cryptically coloured – relying for survival principally upon not being seen – and yet nonetheless display some degree of phenotypic polymorphism. This ranges from the simple tendency towards green and brown morphs in the larvae and pupae of Lepidoptera (Porter, 2010; summarised in Poulton (1890) and Owen (1980)) to *Littorina* winkles or the brittle star *Ophiopholis aculeata* which exhibits variation so extreme that colour ceases to become practical for taxonomic purposes (Moment, 1962; Reid, 1999). Notably in these examples, poly-morphism exists within a single population, distinguishing this phenomenon from local adaptation to different geographical loca-tions in which distinct environmental conditions prevail. Thus, we frequently see variation where, theoretically, we expect con-vergence and uniformity as a result of powerful selective pressure for optimal concealment.

Such cryptic polymorphisms can be divided into two broad groups representing different evolutionary strategies necessi-tated by differences in the interaction between prey, their back-ground and predator perception. These are (1) species inhabiting a fine-grained background which possess a large number of more or less well-defined colour morphs, all of which bear an approxi-mate resemblance to that background (**Figure 1**) and (2) species which inhabit a coarse-grained background possessing relatively few colour morphs, each of which is differentially cryptic on dif-ferent background types (Bond, 2007). While fine-grained back-grounds may or may not be visually complex, they are relatively homogeneous; coarse-grained backgrounds are heterogeneous, consisting of large, internally homogeneous, patches of one back-ground type alongside other visually distinct patches. Many back-grounds will vary in the degree to which they are homogeneous or heterogeneous across a range of absolute scales – a pebble beach, for instance may appear relatively fine-grained to a human observer but would doubtless be rather coarse-grained from the perspective of smaller animals, such as shore birds or marine invertebrates.

In a heterogeneous background (2), organisms tend to be encountered on one patch type at any given moment. Conse-quently, to the degree that the different constituent patches of the background are distinct, selection will be disruptive due to trade-offs in increasing resemblance to any one patch type. Under these conditions, a range of morphs are predicted to evolve, each of which is optimally cryptic on a specific patch type. Throughout the nineteenth and twentieth centuries, the relative frequency of darkened colour forms of various species of Lepidoptera within different populations varied with the degree to which those envi-ronments had been blackened by pollution from industrial pro-cesses, with either form (the light or dark morphs) rarely reaching complete fixation (reviewed by Kettlewell (1973) and Majerus (1998)). Similarly, the phasmid *Timema cristinae* possesses dif-ferent colour morphs which are optimally cryptic on visually distinct host plants (Sandoval, 1994). Termed specialist poly-morphism by Bond (2007), because the constituent morphs of the polymorphism are specialised to one particular patch type, this form of cryptic polymorphism can be understood simply as
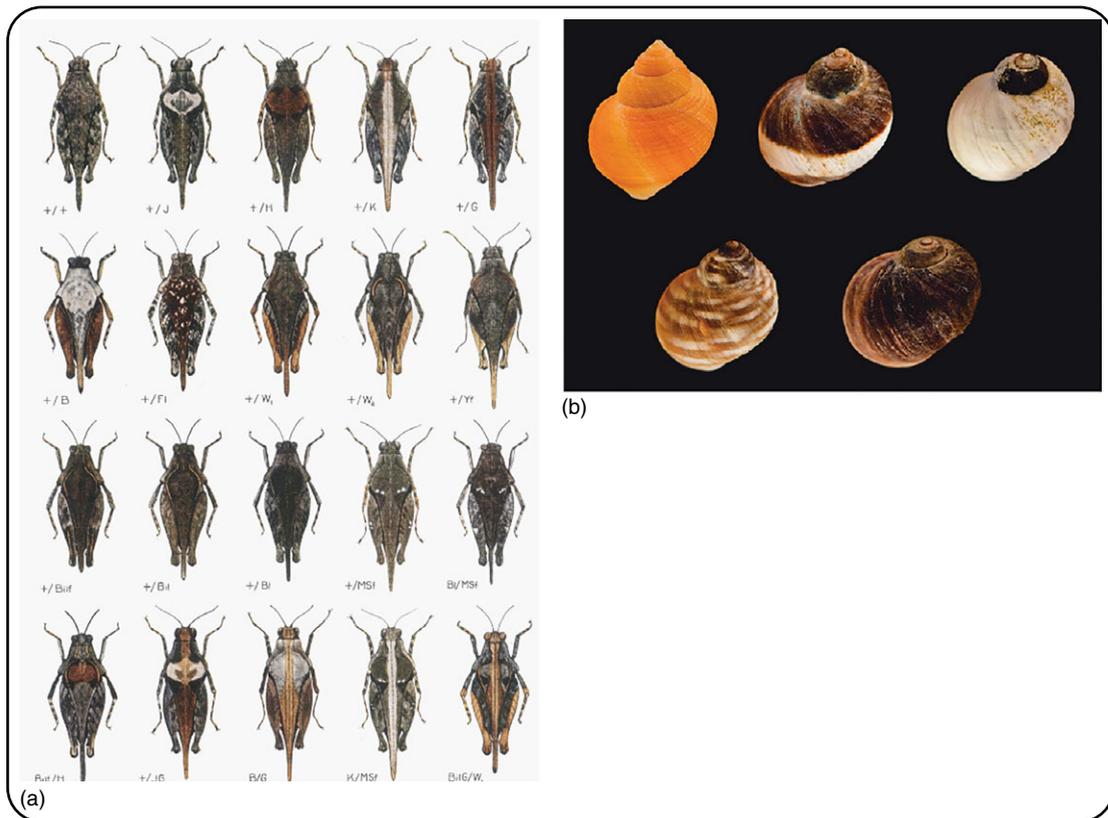
Figure 1 Examples of varying degrees of exuberant or generalist polymorphisms in (a) the locust *Acrydium arenosum* and (b) the rough periwinkle *Littorina saxatilis*. Such species inhabit visually complex but relatively homogeneous environments, lacking large discontinuous patches of different sorts of background. Despite the expectation that selection would produce a single, optimally concealed colour phenotype, these species are extremely diverse in appearance. (a) (b) Reproduced from Nabours, R.K. 1933. Inheritance of color patterns in the grouse locust *Acrydium arenosum* Burmeister (Tettigidae). Genetics 18(2): 159–171 by permission of the Genetics Society of America.Reproduced from Johannesson, K., and Butlin, R.K. 2017. What explains rare and conspicuous colours in a snail? A test of time-series data against models of drift, migration or selection. Heredity 118 (1): 21–30, under the terms of a Creative Commons CC BY licence.

polymorphism being an adaptation to a polymorphic environment (Weir, 2018).

Less easily understood are those species inhabiting a relatively homogeneous, fine-grained background which possess a large number of polymorphic colour forms, all of which are approximately cryptic to varying degrees (1). The intertidal mollusc *Donacilla cornea* represents one such species. It is found along sand or shingle beaches in the Mediterranean and European Atlantic, filter feeding just below the surface of the substrate (Whiteley *et al.*, 1997). It is therefore exposed to predators in a visually complex background environment, but one which is fairly homogeneous, without large contrasting patches of different substrate types. Similarly, the North American forest floor locust *Acrydium arenosum* displays dozens of highly variable cryptic colour morphs (Nabours, 1933) (**Figure 1a**). Despite apparently relying principally on avoiding detection by predators for survival, these species, and many others, have evolved huge numbers of morphs in so-called exuberant (Oxford, 2008) or massive polymorphisms (Owen and Whiteley, 1986) and not a single, optimally cryptic colour pattern. These have been termed generalist polymorphisms (Bond, 2007).

Polymorphism as a Product of Perception

Poulton (1890), in his seminal survey of the functions of animal colours, seems to have been the first to offer a potential explanation for generalist cryptic polymorphisms, although obliquely. In discussing larval dimorphism in Lepidoptera, particularly the green or brown caterpillars of the emerald moth *Geometra papilionaria*, he proposed three possible fitness benefits. Firstly, all the colour forms of such species tend to be, in and of themselves, cryptic, and so protective – greens and browns, as seen in *G. papilionaria,* are, he asserts, 'the chief tints of nature' (p. 46) (also see Owen (1980)). Secondly, species may benefit from being polymorphic as they disperse because certain colour morphs may be differentially cryptic in new areas, with different host plants and environmental conditions. Here, he clearly anticipated the idea of specialist polymorphism (Bond, 2007), noting that the catkins of the host plant on which larvae of *G. papilionaria* feed are themselves either greenish or brownish, presenting a patchy background of two distinct colour habitats. Finally, he argued that

in a species with several colour morphs, 'foes have a wider range of objects for which they may mistake the larvae, and the search must occupy more time, for the equivalent results, than in the case of other species which are not dimorphic' (p. 47). In other words, the range of variation in the appearance of the larvae makes finding them more difficult and protracted for a predator, because the environment must be searched more thoroughly, and as such a member of a polymorphic population would be at an advantage over a member of a monomorphic one. Being different, and deviating from the expectation of a predator, is in and of itself advantageous. However, the fact that polymorphism would disrupt predators in their search for prey is taken as self-evident, and Poulton did not go so far as to articulate the perceptual mechanisms which might lead to this.

The first intimations of such a mechanism are found in a little-known textbook by German biologist Jacob von Uexkull (1934), where he discussed several instances of perceptual mistakes by humans and animals. The classic example is that later recounted by Croze (1970) and Bond (2007), where the author describes staying at a friend's home and having a ceramic jug of water placed at his table every day during lunch. On one occasion, the jug happened to be replaced by a glass carafe and, though placed in its customary location, the author could not see the new water carrier until he was reassured that it was indeed there and, suddenly, though he was staring at the same place as he had before, he at last *perceived* it. Von Uexkull argued that strong psychological expectations held by an organism can actually obscure what it sees – the *suchbild,* or 'search image' (i.e. the idea and mental picture of what one is looking for), overwhelms the actual visual stimulus. Taken to extremes, it is easy to imagine how frequent and indiscriminate overriding of visual stimuli received from the immediate environment by incomplete, imprecise memory could actually be distinctly disadvantageous to an organism (Croze, 1970). Nonetheless, it fits with our subjective experience of the world to say that it is easier to find something when one has a clear mental picture of what one is looking for – perhaps then, search images offer a means of filtering the visual environment, and the sort of perceptual mistakes related by von Uexkull represent the occasional failings of an otherwise adaptive system.

The success of predators in detecting prey is constrained by the ability of their nervous systems to process the visual information being received from the environment they are searching. The rate at which visual information can be neurologically processed is limited (Koch *et al.*, 2006) and is often considerably lower than the rate at which that information is being received (Dukas, 2004). Animals therefore have a finite capacity for attention and must selectively prioritise particular components of incoming information, through a process known as 'attentional filtering'. By definition, therefore, information processing is subject to a trade-off where increased attention devoted to one particular part of the environment occurs only at the cost of other stimuli being perceived at lower resolution or not at all (Dukas and Kamil, 2001; reviewed in Dukas (2004)). In reference to von Uexkull's anecdote, we might call this the 'caveat of the carafe' – his attention was seemingly so heavily engaged in searching for one particular visual stimulus that perception was blinded to what was in fact there. It is significant that the replacement carafe which he failed to perceive was made of colourless glass and so was cryptic to a

degree, or at least not conspicuous. Had it been more conspicuous in manufacture, it may well have been perceived regardless of his reduced attention – the closer the resemblance between an object and its background, the more attentional resources must be devoted to perceive the subtleties which distinguish the one from the other (reviewed in Dukas (2002, 2004)). Equally, the more complex and information-rich the background environment, the more redundant information exists to tax an animal's cognitive apparatus, and the more necessary selective attention and attentional filtering becomes (Dimitrova and Merilaita, 2012). And yet, predators are daily faced with the daunting perceptual task of searching for highly cryptic prey in highly complex visual environments – perhaps the most startling fact is that, in spite of this, somehow they do manage to successfully filter their surroundings and locate sufficient prey. **See also: Neural Information Processing**

The Search Image Concept and the Caveat of the Carafe

In theory, search images represent a behavioural mechanism by which predators might overcome the three factors described above which hinder prey detection: crypsis, which makes prey inherently difficult to discern; the underlying limits on the rate at which visual information can be processed by the nervous system; and, visually complex background environments which overload the nervous system with information. Tinbergen's (1960) work undoubtedly provided the first clear articulation of an adaptive search image concept. He investigated the regulation of insect populations in Dutch pine woodlands and was specifically concerned with the factors affecting the likelihood of an individual insect being found and predated by insectivorous birds. In the course of a study from 1947 to 1954, he quantified the abundance in the environment of various known and putative prey species (mainly coniferophagous moth caterpillars and the caterpillar-like larvae of sawflies) and the composition of food brought by small passerines back to their nests (especially the great tit *Parus major*). If the birds conducted a random search of their environment and consumed any prey items which they happened to encounter, then we would expect that the relative proportion of each prey species in their diet would approximately equal their relative abundance in the environment. However, Tinbergen noted a discernible time lag between changes in the environmental abundance of several common prey species and the expected commensurate change in their representation in the diet of the birds. In addition, at very low densities prey species seemed to be consumed disproportionately infrequently, and at very high densities disproportionately frequently (**Figure 2**).

Attempting to explain these observations, Tinbergen argued that the birds formed a 'specific searching image' of proven prey items previously encountered by chance while searching – the birds were learning the visual features associated with a given prey species (e.g. its morphology, colouration and size) and actively searching the environment with this image in mind so as to improve their chances of finding another such individual. Faced with well-camouflaged prey, occurring at 'very low density, and […] diluted in a tremendous amount of needles and
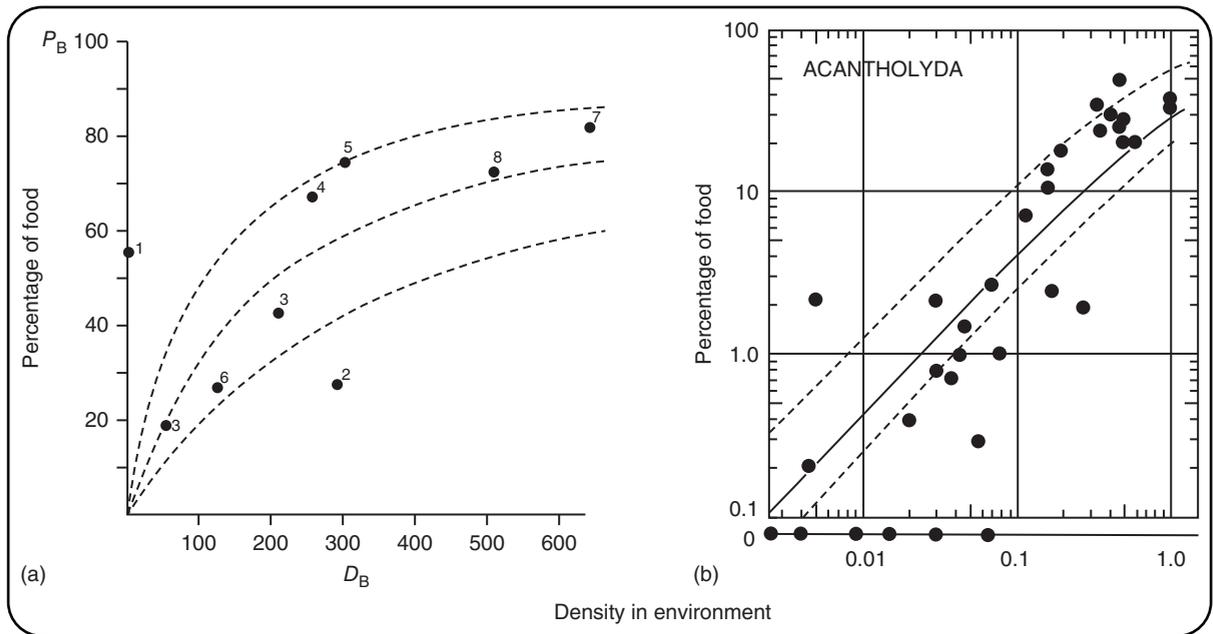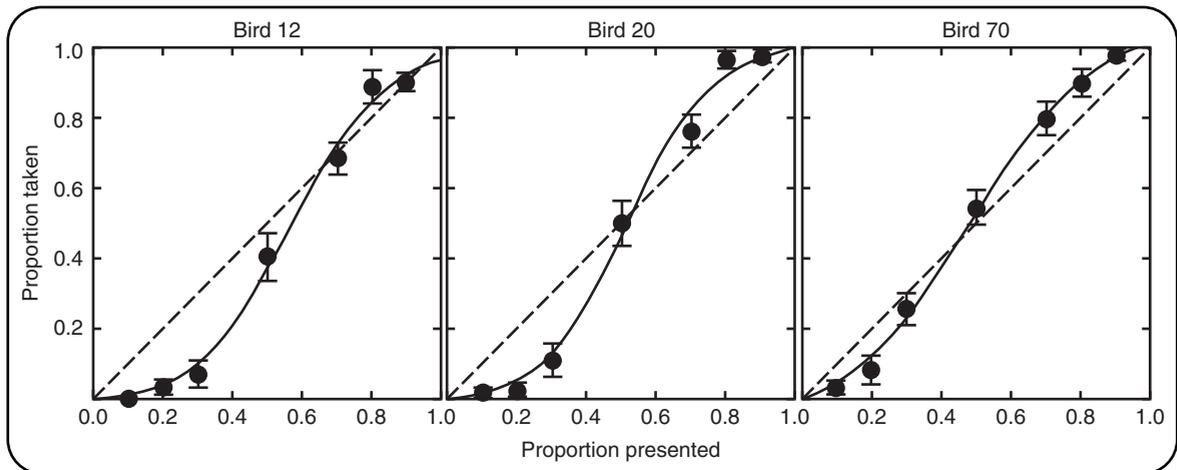
Figure 2 Actual versus predicted predation by tits *Parus* of (a) adult bordered white moths *Bupalus piniaria* and (b) sawfly *Acantholyda* larvae at varying prey densities. Predation of the moths occurred primarily on the forest floor, and sawfly larvae were collected by searching the canopy. Lines represent the expected rate of predation based on a random encounter model with confidence intervals. Points show field collected data. It is evident that at high densities prey are predated disproportionately frequently, while the contrary is the case at low densities. (a) (b) Mook, J.H., Mook, L.J., and Heikens, H.S. 1960. Further evidence for the role of "searching images" in the hunting behaviour of titmice. *Archives Néerlandaises de Zoologie* 13 (3): 448–465. © 1960, Brill Academic Publishers. Tinbergen, L. 1960. The natural control of insects in pinewoods I: factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* 13: 265–343. © 1960, Brill Academic Publishers.

twigs' (p. 334), the birds were performing 'a highly selective sieving [of the] visual stimuli reaching their retina' (p. 332) in order to pick out what they knew, by experience, were the particular visual cues associated with prey. Tinbergen contended that different search images could be utilised in order to optimise foraging performance based on whichever prey species was most abundant at the time, and thus whichever image proved to be most productive. When the returns of hunting to a particular image began to decrease, the birds would enter a cognitively receptive state in which they would switch their in-use search image to that of another prey item encountered during the course of random searching. This produced the distinctive pattern of disproportionate over- and under-predation at high and low densities, respectively (**Figure 2**).

Limitations on the allocation of selective attention mean that predators are likely limited to a small number of search images through which to filter their environment, and that the utilisation of one image occurs only at the cost of decreased efficiency in using another image, or the perception of other stimuli in general (Dukas and Kamil, 2001). Thus, the delay of several days which Tinbergen observed between a prey species becoming abundant within a bird's territory and then later within its diet resulted from a period during which they continued to hunt to an old, now unprofitable, search image (of a species no longer most abundant in the environment), before a new image was adopted. Consequently, they failed to perceive alternative, visually distinct prey items, because their limited attention was already heavily

engaged – this is the caveat of the carafe trade-off in operation. Working with Tinbergen, but on a different prey type in a distinct woodland microhabitat, Mook *et al.* (1960) were simultaneously able to corroborate Tinbergen's evidence to a remarkable degree (**Figure 2**).

It is clear that Tinbergen (1960) saw his '*specific* searching images' (my emphasis) as quite literally the learned visual characteristics of different *species*. Considering the concept logically, however, there is no reason why the predators might not form and deploy search images of visually distinct groups within a species, such as the constituent morphs in a prey polymorphism (Clarke, 1962). Indeed, the sole criteria for the formation of a search image is the visual distinctness of a prey type – the breadth or narrowness of the strictly biological taxa encompassed by that image will vary with the ability of the predator to discriminate between them (Croze, 1970). The utilisation of that image rests only on the returns of its employment continuing to exceed the potential missed opportunities resulting from the tendency to overlook alternative prey (Bond, 1983; modelled mathematically in Dukas and Ellner (1993)) (**Figure 3**). If a polymorphic prey species were common enough such that it was profitable for predators to hunt to a search image of one particular, visually distinct colour morph in that species, it follows that a novel colour form would be at an advantage because a predator would be less likely to perceive it since it does not conform to the in-use search image. This is not to say that predators would ignore rare colour forms, but rather that, like the glass carafe, they would not see

Figure 3 Actual versus predicted predation of visually distinct grain types on a cryptic background by captive pigeons. Grains were provided in dimorphic populations at varying relative morph proportions. Where predation is entirely random, we would expect the proportion of each 'prey' type taken to approximately equal its abundance in the population, such that the proportion taken and the proportion presented ought to be equal. This expectation is illustrated by the dashed line. In these experiments, birds biased their predation to the most common grain type, such that they were predated disproportionately frequently. This is consistent with their using search images to optimise foraging. Bond, A.B. 1983. Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. Journal of Experimental Psychology: Animal Behavior Processes 9 (3): 292–306. © 1983, American Psychological Association.

them or recognise them as visually distinct from the background. The allocation of attention to searching for one image makes other visual stimuli more likely to become lost in the noise of information being received as 'background'. The use of search images would therefore result in a very specific form of negative frequency-dependent selection on intraspecific colour morphs in abundant prey species, which Clarke (1962) christened 'apostatic selection'. Deviant ('apostate') colour forms, while at a selective advantage, cannot be different to the extent that they are no longer generally cryptic, for a highly conspicuous morph might be found fairly easily by predators without the need to dedicate consider-able attentional resources using a search image (Dukas and Ellner, 1993; Dukas, 2002). The combined selective pressures favouring increased cryptic resemblance on the one hand and phenotypic novelty on the other offer a possible explanation for the existence of general cryptic polymorphisms in common prey species, with a great number of more or less cryptic colour forms. These apo-static polymorphisms would therefore be a direct adaptation to the perceptual and behavioural mechanisms of the predators in question and a means of thwarting their search images. **See also: Selection: Frequency-dependent**

The Complex and Incomplete Evidence for Apostatic Polymorphisms

The mechanism by which search image use might drive the evolution of phenotypic polymorphism can be decomposed into several distinct but interdependent hypotheses: that search images are employed by predators while looking for prey;

that the use of search images extends in a meaningful way to intraspecific colour morphs; that the use of search images exerts negative frequency-dependent (apostatic) selection on the constituent morphs of intraspecific polymorphisms; and, that search image-driven apostatic selection actively maintains polymorphisms in wild prey populations (Weir, 2018). I have already discussed some of the evidence which Tinbergen (1960) advanced in support of search images though it has been argued, with some justification, that he went beyond what could be reasonably concluded from his data (Bond, 2007). Many of the conceptual notions underpinning search images had been established previously (Poulton, 1890; von Uexkull, 1934), and modern work continues to demonstrate the necessity for selective attention when animals conduct search tasks in natural environ-ments (reviewed in Dukas (2004)), providing the underlying constraint which is the basis for their use (Dukas and Kamil, 2001; Karpestam *et al*., 2014). However, it does not necessarily follow that animals do allocate attention in the way described by the search image hypothesis – this hypothesis makes a very specific claim not only about how an animal interacts with its environment but how it actually perceives it (Lawrence and Allen, 1983). The difficulty, therefore, lies in distinguishing in operational and experimental terms between a simple preference, proclivity or coincidental bias for one prey type over another, and a predator actually *learning to see* a cryptic prey item using a search image, which it would have otherwise failed to perceive (Krebs, 1973).

Guilford and Dawkins (1987) argued powerfully that all the evidence accumulated up to that date purporting to provide sup-port for the existence of search images could equally well, and perhaps even more parsimoniously, be explained by predators adjusting the rate at which they searched the environment for prey

(the 'search rate adjustment hypothesis', see the section titled 'Glossary'). Many studies claiming to demonstrate search image use involve animals having become habituated by the experimenters to one particular prey item, and subsequently showing reluctance to take novel prey items (Beukema, 1968; Ware, 1971). Search images may be involved to an extent, but the results may also simply be due to preference for familiar prey, also called dietary wariness or neophobia (Krebs, 1973). Interestingly, mathematical modelling has suggested that dietary wariness in predators alone could present a distinct and powerful source of negative frequency-dependent selection on polymorphic populations (Franks and Oxford, 2009). Indeed, a great deal of work exists which shows that predators can exert frequency-dependent selection on polymorphic populations (reviewed by Allen (1988)), though the precise cause of that selection is often far from clear. The 'prey' in such experiments are often highly conspicuous artificial baits, and it is unlikely that search images would even operate under such conditions (Dukas and Ellner, 1993) – visually obvious prey require far less attentional filtering to spot. Regardless, these studies demonstrate that many predators do possess the underlying cognitive ability to recognise and distinguish morph-specific phenotypic characters, which the search image and apostatic selection hypotheses presuppose (Tinbergen, 1960; Clarke, 1962).

A preeminent problem with experimental studies which purport to investigate the concept of search images and their population-level effects is that they often employ very artificial 'prey' items, captive predators or simply unnatural experimental environments (summaries given by Krebs (1973), Allen (1988) and Bond (2007)). This is undesirable if the aim is to make behavioural observations and extrapolate to natural environments. Some of the most interesting, though seldom cited, support for search images comes from Majerus (1978, 1998). He presented flocks of starlings *Sturnus vulgaris* with recently killed larvae of the angle shades moth *Phlogophora meticulosa* at low density, in dimorphic green and brown populations, and at varying relative morph frequencies. Larval populations were replenished daily, and across several days the ratio of common to rare morphs consumed increased markedly, regardless of which colour morph was most common. This is powerful evidence because although the likelihood of encountering a rare morph did not decrease, the birds seemed increasingly prone to overlook them – under this experimental set-up, it is difficult to formulate an alternative explanation other than that they were developing and utilising a profitable search image (Majerus, 1998). Generalising these results to wild populations of *P. meticulosa* larvae, it follows that the rarer morph would be at a selective advantage and supports the apostatic selection hypothesis. Other recent experiments involving the 'predation' of prey images generated on computer screens by captive blue jays *Cyanocitta cristata* have provided further, compelling evidence of search image behaviour in action and its resulting in apostatic selection. Predation across prey 'generations', with programmes simulating morph genetics, resulted in the evolution of increasingly elaborate phenotypic polymorphisms (Bond and Kamil, 1998, 2002) (**Figure 4**). Notably, this effect is observed most strongly in homogeneous but complex background environments, which necessitate an increased use of selective attention in a search
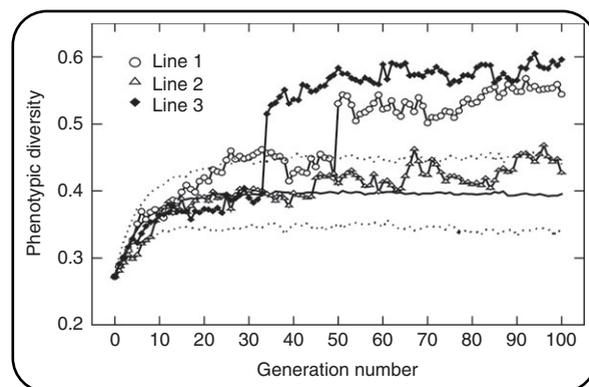
Figure 4 The effects of selection by blue jays on phenotypic variation in populations of digital moth-like prey items. Lines 1, 2 and 3 represent different experimental lines (i.e. replicates). The solid black lines (and finely dashed lines) show estimated results (and 95% confidence intervals) where selection was frequency independent and favoured increased cryptic resemblance to the background. Phenotypic diversity of the artificial moth populations was recorded across each generation. Computer programmes simulated the genetics and evolution of each population based on predation results. In all cases, natural predation by jays ultimately results in higher levels of phenotypic variance across the generations than is expected where the sole selective pressure is for increased background resemblance. This suggests that the moth-like targets of predation derive some fitness benefit from deviating from the norm, as well as from resembling their background, consistent with the effects of search image-driven apostatic selection. Bond, A.B. 2002. Visual predators select for crypticity and polymorphism in virtual prey. Nature 415 (6872): 609–613. © 2002, Springer Nature.

task and provide the circumstances under which we predict search image behaviour to operate most strongly (Bond and Kamil, 2006).

It is much harder to make the jump to natural populations and show that apostatic selection is a significant force in nature which actively evolves and maintains phenotypic polymorphisms. Many generalist cryptic polymorphisms are maintained by negative frequency-dependent selection, as opposed to other forces (such as heterozygote advantage) (Clarke, 1962; Johannesson and Butlin, 2017), but this is not precisely proof of their being maintained by *apostatic selection* (Weir, 2018). However, in one group of British moths where polymorphism is thought to have evolved due to search image use (Kettlewell, 1973; Majerus, 1998), it has been shown that there is a strong positive correlation between the abundance of a species and the degree to which it is polymorphic (Weir, 2018). This is exactly what we would expect where abundant species most reward the use of search images against individual morphs and as such would be subject to the greatest force of apostatic selection. This perhaps offers us a glimpse into the operation of this mechanism in natural populations and an avenue for future research.

The concept of search images has natural appeal, and the expansive literature which has grown up around it is testament to its elegance. I have throughout, for simplicity, treated the deployment of search images as an attribute of searching predators, but any animal engaged in a complex visual task might use them. Concealed predators may themselves benefit from phenotypic novelty where their prey are scanning the environment using search

images (Fowlie and Kruger, 2003). Even within a given species, apostatic selection can operate, for example in damselflies where novel female colour morphs, which benefit from reduced rates of detection and sexual harassment by males, are favoured (Fincke, 2004). These last two points emphasise that the overall picture is an exceedingly complex one. To conclude, while there is a great deal of work suggesting that search image use, via apostatic selection, can, and does, drive the evolution of phenotypic polymorphism, a comprehensive review and evaluation of that evidence – and its deficiencies – is sorely lacking.

Glossary

Apostatic selection Coined by Clarke (1962), this refers to very specific cases of negative frequency-dependent selection on one species resulting from the use of search images by another species. To increase foraging efficiency, predators adopt search images of the most abundant morphs of a common polymorphic prey species, hunt to this image and therefore fail to perceive the rarer morphs, which puts them at a selective advantage. It is unfortunately often used synonymously with negative frequency-dependent selection in the literature – for clarity, I have herein restricted its usage to the original definition and would actively encourage others to do so to minimise potential future misunderstanding.

Crypsis From the Greek κρυπτὸς, meaning hidden. Often called camouflage, crypsis describes the broad ability of an organism to avoid detection by other animals and may be used by both predators and prey. Organisms which display cryptic colouration are coloured and patterned so as to resemble their environment and avoid or reduce the likelihood of visual detection. Though the fact is seldom emphasised, crypsis should properly be defined in relation to the perceptual apparatus of the species which is the target of the deception, since this dictates the selective pressures in operation. Different forms of colour vision, for example could result in different colour patterns against the same background. Cryptic colouration often involves a resemblance to a random sample of the environment in which the cryptic animal is most often encountered by the organism it is seeking to deceive (Endler, 1981). I do not discuss forms of crypsis other than those related to colouration in this article and so for simplicity use the term interchangeably with the more specific 'cryptic colouration'. The term 'crypticity' describes the degree of crypsis.

Generalist and specialist polymorphism In specialist polymorphisms, the constituent morphs each match different, visually distinct patches of background in the environment. Generalist polymorphisms consist of a large number of morphs, all of which bear an approximate resemblance to the mean environmental background. This terminology was coined by Bond (2007), and follows that established by Poulton (1890), for example specialist crypsis as a resemblance to a particular object or component of the environment (such as a leaf or twig), and generalist crypsis as simply adopting the general hue and patterning of the environment as a whole (such as being white or green in arctic or forest environments, respectively).

Phenotypic polymorphism Where individuals within a population can be divided into two or more discontinuous phenotypic forms or 'morphs'. Transient polymorphisms occur when selective pressures acting on a population change, and a novel or previously disadvantageous morph arrives at a selective advantage, such that the previously dominant, now disadvantageous morph, is gradually supplanted. For a period of several generations, therefore, both morphs coexist within the population. Selective pressures determine the speed at which the new morph spreads and reaches fixation. A notable example of transient polymorphism is industrial melanism in Lepidoptera (Kettlewell, 1973). Polymorphism may also be balanced, where each morph is maintained in the population at an equilibrium frequency based on the competing selective advantages and disadvantageous of each. The most obvious example of balanced polymorphism is the maintenance of two sexes in a population (Ford, 1964).

Search image A mechanism by which animals might filter a visually complex environment to detect an inconspicuous object and overcome the limited information processing abilities of their nervous systems. Search images are the recalled visual impression of an object encountered previously, which is used when searching the environment to increase the probability of encountering another such item, thus increasing foraging efficiency. The logic of the concept can be summed up as it being easier for an animal to find something if it has a clear, specific mental image of what it is looking for (as opposed to more abstract ideas such as simply 'food' or 'insects').

Search rate adjustment hypothesis First proposed by Gendron and Staddon (1983), it describes, in contrast to search image use, an alternative means by which predators searching for concealed prey in a visually complex environment might increase their foraging efficiency. Predators are faced with a trade-off between the quantity of ground they can cover during a search and the thoroughness with which they can visually search that ground – they may search a small area very thoroughly or a large area more cursorily. Searching for conspicuous prey will occupy less time than for more highly concealed prey, because less attention need be applied to a given area in order to detect them. Thus, predators may optimise foraging by adjusting the rate at which they search the environment based on the relative crypticity of the prey for which they are searching. Where prey are polymorphic, predators will therefore exert negative frequency-dependent selection on the various colour morphs by searching the environment at a rate which maximises detection of the most abundant prey morph. Such behaviour may produce results superficially suggestive of apostatic selection (Guilford and Dawkins, 1987). However, the logic of the search rate adjustment hypothesis implies that where two morphs are equally cryptic, they will be detected optimally at the same search rate. Thus, in a population of several equally cryptic morphs, we would not expect negative frequency-dependent selection on morph frequency if predators hunted by adjusting their search rate, but would expect to see it (as apostatic

selection) where predators utilised search images – one search image interferes with the detection of other prey morphs, regardless of relative crypticity (except where morphs are so conspicuous as to not require their use for detection), but a given search rate applies equally well to all equally cryptic morphs. I have previously shown, in artificial moth populations predated by wild birds, that polymorphic populations of equally cryptic morphs are in fact subject to negative frequency-dependent predation, supportive of the apostatic selection hypothesis (Weir, 2018).

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