

## REVIEW

# Reasons to be different: do conspicuous polymorphisms in invertebrates persist because rare forms are fitter?

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**Abstract**

Many invertebrate species show conspicuous colour polymorphisms, the study of which has provided us with important insights in evolutionary biology. The potential importance of frequency-dependent selection in the maintenance of polymorphisms was identified by theoretical studies more than 50 years ago, and since then, the topic has received considerable attention from those seeking to explain observed diversity in natural populations. Here, we consider the different ecological interactions that have been shown to lead to negative frequency-dependent selection in invertebrate populations in the wild, and assess the likely relative importance of this mechanism in comparison with alternatives that may promote genetic and phenotypic diversity. The literature shows that frequency dependence can result from a wide array of ecological interactions, in particular, those involving mate choice, sexual conflict and predation. However, even though negative frequency-dependent selection is the most common explanation for the occurrence of conspicuous polymorphisms in invertebrates, conclusive evidence of its importance in natural populations is largely absent. A particular problem is that in most studies, it is the only explanation considered. In the most comprehensively studied systems, it has been shown that multiple mechanisms (both selective and neutral) operate to maintain observed phenotypic variation, and that negative frequency-dependent selection is not the most important of these. Thus, as yet at least, we do not have strong grounds for believing that negative frequency-dependent selection is a major diversifying force in invertebrate morphology. However, without more comprehensive studies in a wider range of ecological contexts, we are equally unable to dismiss it as weak and/or irrelevant.

**Introduction**

Polymorphism occurs when two or more genetically and phenotypically different forms, known as morphs, can be found in a single interbreeding population, with the rarest one occurring at frequencies that are too high to be maintained by mutation alone (Ford, 1945). It has long represented an evolutionary puzzle, because alternative forms are expected to vary in fitness, and those with lower fitness should be eliminated by natural selection (Darwin, 1883; Fisher, 1930). The fact that different morphs do indeed persist alongside one another in many populations (Brockmann, 2001; Bond, 2007; Gray & McKinnon, 2007; Mitchell-Olds, Willis & Goldstein, 2007; Kunte, 2009), remains a central problem in evolutionary biology.

While non-selective processes have been invoked to explain the maintenance of polymorphisms (e.g. the fitness differences among morphs could be negligible), in many cases, it is thought that local selective processes, with or without gene

flow among populations, must be involved (King & Lawson, 1995). Several selective mechanisms, such as disruptive selection and heterozygote advantage, are likely to play a role, but frequency-dependent selection is perhaps the most commonly cited explanation for observed polymorphisms (Brockmann, 2001; Gray & McKinnon, 2007; Mitchell-Olds *et al.*, 2007). Negative frequency-dependent selection (NFDS), in which a rare morph has a fitness advantage over common morphs, can account for the existence of different morphs at stable frequencies in a population (Clarke & O'Donald, 1964; Ayala & Campbell, 1974), and has been proposed to explain polymorphisms in a number of contexts (Hori, 1993; Fincke, 2004; Sinervo & Calsbeek, 2006; McKillup & McKillup, 2008; Hampton, Hughes & Houde, 2009; Koskella & Lively, 2009). Evidence of NFDS has been observed both in laboratory (Kojima & Tobari, 1969; Maskell, Parkin & Verspoor, 1977; Anderson & Brown, 1984; Gigord, Macnair & Smithson, 2001; Fitzpatrick *et al.*, 2007; Koskella & Lively, 2009) and natural conditions (Reid, 1987; Hori, 1993; Svensson, Abbott

& Hardling, 2005; Olendorf *et al.*, 2006; Bleay, Comendant & Sinervo, 2007; McKillup & McKillup, 2008; Takahashi & Watanabe, 2010). Nevertheless, considerable uncertainty exists about the relative importance of this and other mechanisms in the maintenance of genetic and phenotypic diversity in real populations.

There are some genetic polymorphisms that do not affect phenotypic traits. They occur in non-coding areas of the genome, and have been used as markers for studies in population genetics, evolution and medicine (Hacia *et al.*, 1999; Jorde *et al.*, 2000; Syvänen, 2001; Williamson *et al.*, 2007). Polymorphisms that do affect phenotypic traits are not always apparent to the observer, such as some of those involving behaviour and resistance to parasites or diseases (Thornhill, 1979; Field & Keller, 1993; Kirkup & Riley, 2004; Duncan & Little, 2007; Laine & Tellier, 2008). In contrast, conspicuous polymorphisms, particularly those involving colouration, are easy to score, and their study has been central in attempts to understand the mechanisms that could be maintaining genetic and phenotypic variation in populations. Colouration is known to serve an adaptive function in processes such as thermoregulation (Quartau & Borges, 1997; Phifer-Rixey *et al.*, 2008), attraction of mates (Nielsen & Watt, 2000), avoidance of predators (Hoese *et al.*, 2006) and attraction of prey (Hauber, 2002; Heiling *et al.*, 2005; Bush, Yu & Herberstein, 2008). This strongly suggests that the maintenance of conspicuous colour polymorphisms is influenced by selection, and NFDS in particular has often been assumed to play a key role.

Many species of insect, mollusc, arachnid and crustacean display conspicuous and easily measured polymorphic colour traits. Such invertebrates are typically easier to manipulate than vertebrates, both in the field and in the laboratory, and it is relatively easy to get large sample sizes. As a result, many of the most detailed case studies of the potential influence of NFDS on traits come from the study of colour-polymorphic invertebrates. In this review, we consider the different ecological interactions that have been hypothesized to generate NFDS in these studies, and evaluate the evidence that NFDS actually plays a role in maintaining colour polymorphisms in invertebrates. We then discuss its relative importance in comparison with alternative mechanisms that could be maintaining genetic and phenotypic diversity.

## NFDS

The idea that the fitness of an organism is affected by the relative frequencies of the genotypes in a population was first described by Fisher (1930), suggesting that an inverse relation between the two could maintain stable polymorphisms. This concept was later formalized by other researchers, such as Li (1955), Wright (1956) and Lewontin (1958), who developed mathematical models to describe the mechanism.

Evidence that the fitness of a morph depends on its frequency relative to the frequencies of the other morphs was first found by Wright & Dobzhansky (1946) in an experimental population of *Drosophila pseudoobscura*. Three different gene arrangements can be found in the third chromosome of this

species, and their frequencies were observed to fluctuate over the year in natural populations. Wright and Dobzhansky set up an experimental population with known frequencies of the different genotypes and controlled environmental conditions. They found that the observed changes in frequencies of the phenotypes at different temperatures fitted the predictions of a model where the fitness of the homozygotes decreases as their frequencies increase, while the fitness of the heterozygotes remains constant. However, Wright and Dobzhansky considered this hypothesis to be an 'extreme' one. Since then, there have been several laboratory studies where evidence for NFDS has been found in populations of *Drosophila*, with morph frequencies fluctuating in a manner that is predictable based on the known effects of frequency on fitness (Levene, Pavlovsky & Dobzhansky, 1954; Kojima & Tobari, 1969; Anderson & Brown, 1984; Singh & Chatterjee, 1989). A correlation between fitness and frequency has also been found in laboratory studies in crustaceans (Maskell *et al.*, 1977; Duncan & Little, 2007), land snails (Tucker, 1991) and water snails (Koskella & Lively, 2009). This correlation has been found in natural populations as well, and is the commonest form of evidence supporting NFDS in the wild (Reid, 1987; Gross, 1991; Seehausen & Schluter, 2004; Svensson *et al.*, 2005; Olendorf *et al.*, 2006; Bleay *et al.*, 2007; Takahashi & Watanabe, 2010). A few studies have also demonstrated oscillations in morph frequencies over time that can be explained by NFDS (Hori, 1993; Sinervo & Lively, 1996). However, direct evidence for NFDS in the wild is generally scarce because the best way to test for it is to manipulate the frequencies of different morphs in a population, and to obtain reliable measures of fitness from individuals of each morph, both of which pose considerable practical challenges. Even though these complications should be easier to overcome in laboratory conditions, a comprehensive experimental test of the hypothesis with real organisms is yet to be published, and the most unequivocal demonstration of NFDS acting to maintain polymorphism comes from a study involving selection by real predators (birds) on polymorphic computer-simulated prey (Bond & Kamil, 1998; Bond & Kamil, 2002).

Although we do not have definitive evidence that NFDS maintains diversity in wild populations, there is a growing body of research that demonstrates the potential for various ecological interactions to generate NFDS. Sexual interactions between conspecifics, interactions among competitors, and trophic interactions between natural enemies and their prey/hosts, have all been documented as having frequency-dependent effects on the fitness of morphs in natural populations (Brockmann, 2001; Sinervo & Calsbeek, 2006).

## Male–female interactions

Sexual interactions between males and females may lead to NFDS and, as a consequence, maintain balanced polymorphisms in populations. In particular, and for obvious reasons, it has frequently been assumed that sexual interactions are implicated in the maintenance of sex-limited polymorphisms, where one sex (usually the female) exhibits conspicuous variation in colour, while the other is monomorphic. However,

negative frequency-dependent sexual selection has also been identified in species in which polymorphism occurs in both sexes. There are, broadly speaking, two kinds of hypothesized explanations involving NFDS and sex in the maintenance of diversity, which correspond to two different kinds of sexual interaction: sexual conflict and mate choice (Brockmann, 2001).

### Sexual conflict

Sexual conflict occurs when males and females have different interests in the outcome of sexual encounters, and this can result in adaptations that counteract each other. One way in which such conflict may lead to NFDS stems from harassment of females by males. If a female receives a significant number of unwanted mating attempts by males, this can generate costs for her in terms of time, energy, fecundity, foraging, longevity and predation risk (Arnqvist, 1989; Odendaal, Turchin & Stermitz, 1989; Krupa & Sih, 1993; Rowe, 1994; Stone, 1995; Clutton-Brock & Langley, 1997; Jormalainen, Merilaita & Riihimäki, 2001). In order to avoid these costs, females can evolve alternative strategies that may have a fitness advantage depending on the frequency of either the other female strategies or of the males in the population (i.e. the sex ratio).

NFDS caused by male harassment of females has been extensively researched in damselflies (Van Gossum, Sherratt & Cordero-Rivera, 2008; Svensson *et al.*, 2009). In this group, there are several species that show a female-limited colour polymorphism, with two or more discrete morphs, at least one of which is easily distinguished from the male (known as the gynomorph or heteromorph) and at least one of which resembles the male (the andromorph) (Johnson, 1975). Male harassment has been shown to decrease the fitness of females in several damselfly species (Sirot & Brockmann, 2001; Svensson *et al.*, 2005; Bots *et al.*, 2009; Takahashi & Watanabe, 2010), leading to discussion of the role of selection in the maintenance of the observed polymorphism. More specifically, two hypotheses are commonly suggested to explain how NFDS might be involved: the learned mate recognition hypothesis (LMR) and the male mimicry hypothesis (MM).

The LMR hypothesis posits that males will prefer to mate with females of the morph that they encounter more frequently in the population, because they will become more efficient at recognizing them as potential mates (Miller & Fincke, 1999; Fincke, 2004). This effect of female morph frequency on the efficiency of searching males could arise if males rely on a 'search image' (see Effects of Predators on Prey section later) in order to locate potential mates, in which case changes in male preference through 'perceptual switching' may occur if males encounter different female morph frequencies in different locations and/or at different times (Fincke, 1994, 2004; Van Gossum, Stoks & De Bruyn, 2001). A predicted consequence of frequency-dependent male mate-finding efficiency is that females of the common morph will suffer higher levels of male harassment than females of the rare morph, and have lower fitness as a result. This hypothesis thus suggests that andromorphs exist simply because they are different from heteromorphs, and not because there is any

special advantage in resembling a male. Evidence supporting LMR has been obtained from studies in the laboratory and in natural populations in different species of damselflies (Fincke, 1994; Miller & Fincke, 1999; Van Gossum *et al.*, 1999; Van Gossum, Stoks & De Bruyn, 2001; Takahashi & Watanabe, 2009; Takahashi & Watanabe, 2010). Additionally, a strong correspondence has been found among the predictions of simple models based on the type of frequency dependence likely to result from LMR and morph dynamics in natural populations over several years (Svensson *et al.*, 2005; Takahashi & Watanabe, 2010). The conclusion of these studies was that simple NFDS resulting from increased harassment of a common female morph can explain the indefinite persistence of polymorphisms in at least some damselfly populations.

LMR could also occur in some species of colour-polymorphic butterflies, where males have been observed to show a preference for the common female morph (Cook *et al.*, 1994; Nielsen & Watt, 2000; Kemp & Macedonia, 2007). There is, however, no evidence that male harassment reduces the fitness in these species, and in general, our understanding of the different mechanisms that may be involved in the maintenance of the observed morphological diversity in butterflies is less well-developed than in the better-known damselfly systems.

In contrast to the LMR hypothesis, the MM hypothesis proposes that andromorph females gain a fitness advantage by mimicking the appearance and/or behaviour of males. There are several versions of the MM hypothesis discussed in the context of damselfly polymorphism (Johnson, 1975; Robertson, 1985; Hinnikint, 1987; Sherratt, 2001), but those that involve NFDS all assume that frequency dependence in female morph fitness arises because andromorph mimicry is most effective when heteromorphs are relatively common, such that it benefits males to focus their attention on heteromorphs rather than waste their efforts on individuals that may turn out to be males. The key difference from the LMR hypothesis is that, because mimicry is the source of frequency dependence, there is no equivalent frequency-dependent advantage for heteromorphs when they are rare – they are assumed always to be readily identifiable as mates. Instead, the MM hypothesis assumes that there is some frequency-independent cost borne by the andromorphs: either they are more likely to be attacked by predators than heteromorphs because they are less cryptic (Robertson, 1985), or they are more likely than heteromorphs to be encountered by males, because they are more conspicuous or behave more like males (Sherratt, 2001).

Several studies have found evidence that appears to support the MM hypothesis (Sirot *et al.*, 2003; Rivera & Sánchez-Guillén, 2007; Hammers & Van Gossum, 2008; Van Gossum *et al.*, 2011), but in some cases, the reported data are also consistent with the LMR hypothesis (Ting *et al.*, 2009). Hence, the need for predictions that are unique to one or the other hypothesis, and experimental studies, which can test those predictions, has been highlighted (Sherratt, 2001; Van Gossum & Sherratt, 2008). Because LMR is based on males learning to recognize the common female morph as a mate, this morph should always receive a higher number of mating

attempts. In contrast, the MM hypothesis does not predict that the common morph will always receive more mating attempts, but instead, it predicts (uniquely) that andromorphs should be less harassed when they are rare relative to males, and hence that under equilibrium conditions andromorphs should be relatively more common in populations where the sex ratio is male biased (Sherratt, 2001; Van Gossum & Sherratt, 2008). Although both of these predictions have some empirical support (Hinnekindt, 1987; Cordero, 1992; Forbes, Richardson & Baker, 1995; Hammers & Van Gossum, 2008), the problem with testing them in real populations is that female morph frequency may correlate with sex ratio in the wild (e.g. Hammers & Van Gossum, 2008), making it difficult to disentangle cause and effect. A more fruitful line of enquiry may be to examine male behaviour in more detail. There are two studies where andromorph females have been observed to behave similarly to males, and males have responded to them as if they were other males, suggesting that they might actually be fooled by andromorphs (Andrés, Sánchez-Guillén & Cordero-Rivera, 2002; Sirot *et al.*, 2003).

Even though both the LMR and the MM hypotheses are plausible explanations for the patterns observed in natural populations of polymorphic damselflies, each with some empirical support, and notwithstanding the widespread perception that NFDS is likely to be central to explaining sex-limited polymorphism (see, e.g. Van Gossum & Sherratt, 2008), there are several plausible alternative hypotheses that do not involve frequency dependence at all. One of these proposes that andromorphs will have an advantage at high population densities by mimicking males, and this advantage will be offset by the risk of not mating at all at low densities (Hinnekindt, 1987). Very few studies have considered this hypothesis, and no supportive evidence has been found (Cordero-Rivera & Egido-Pérez, 1998). An alternative hypothesis suggests that andromorphs will benefit from avoiding interspecific matings, while paying the cost of higher vulnerability to predation (Johnson, 1975). However, it is not clear how andromorphs would be more efficient than heteromorphs at avoiding interspecific matings, data supporting this hypothesis are lacking, and the trade-off would have to be perfectly balanced for polymorphism to persist at equilibrium. Abiotic factors could also play a role in the maintenance of the polymorphism. Morph frequencies have been observed to vary across geographical ranges where climatic conditions differ (Van Gossum *et al.*, 2007; Hammers & Van Gossum, 2008; Gosden, Stoks & Svensson, 2011), and it has been found that ambient temperature affects mass and protein content of female morphs differently (Bots *et al.*, 2009). It has also been observed that spatiotemporal patterns of morph frequencies do not always correlate with estimates of male harassment (Van Gossum *et al.*, 2007; Hammers & Van Gossum, 2008; Iserbyt *et al.*, 2010). It is thus plausible that different morphs are at a selective advantage in different populations, and that gene flow among those populations maintains diversity in each. Additionally, recent studies suggest the effects of multiple mechanisms, selective and stochastic, acting simultaneously, and varying in time and space (Iserbyt *et al.*, 2010; Sánchez-Guillén *et al.*, 2011; Iserbyt, Van Gossum & Stoks,

2012). However, these hypotheses have not been well explored in damselflies, or other species in which there are sex-limited polymorphisms, and much of what we know about the potential for climatic selection and the interplay of multiple mechanisms to maintain diversity comes from a rather different example of an invertebrate colour polymorphism: that seen in the land snails of the genus *Cepaea* (Cook, 1998; Cameron & Pokryszko, 2008), which is discussed later in this review.

## Mate choice

Mate choice could lead to NFDS, and consequently, to the maintenance of balanced polymorphisms, when either females or males prefer to mate with a rare morph of the opposite sex. An obvious possible advantage of mating with a type of the opposite sex that is not encountered frequently in the population would be to reduce genetic incompatibility from mating with an individual that is genetically similar, or to avoid mating with the same individual more than once (Tregenza & Wedell, 2000; Zeh & Zeh, 2003). This can happen through disassortative mating, where individuals of a particular morph choose to mate with an individual of a different morph more frequently than would be expected under random mating (e.g. in the scarlet tiger moth *Panaxia dominula*; Sheppard, 1952). A form of disassortative mating that is particularly potent in generating NFDS is the 'rare male effect', when females prefer to mate with males of a type that has not been encountered before, such that the rare male morph in the population will have a mating advantage over the common morph (Knoppien, 1985).

The rare male effect has been predominantly studied in the guppy, *Poecilia reticulata*, within the vertebrates (Hughes *et al.*, 1999; Zajitschek, Evans & Brooks, 2006; Hampton *et al.*, 2009), and in *Drosophila* within the invertebrates (Pruzan & Ehrman, 1974; Spiess & Schwer, 1978; Anderson & Brown, 1984; Singh & Chatterjee, 1989; Depiereux *et al.*, 1990; Terzić *et al.*, 1996; Som & Singh, 2005), and it has been found that at least in some circumstances, females do prefer to mate with uncommon males. However, a review by Partridge (1988) pointed out that many studies testing the rare male effect in *Drosophila* were flawed. She argued that most of the experiments suffered from observer bias, lack of repeatability and had problems with experimental design and data analysis. More recent studies in *Drosophila* species, however, with improved experimental design, still support the existence of a rare male effect in cases of both conspicuous (i.e. colour) and cryptic polymorphisms (Singh & Chatterjee, 1989; Depiereux *et al.*, 1990; Terzić *et al.*, 1996; Singh & Som, 2001; Som & Singh, 2005).

The rare male effect has also been observed to occur in the two-spotted ladybird *Adalia bipunctata*. This species shows a polymorphism in the colour and pattern of the elytra and the pronotum, which can range from red to almost completely black, and the frequencies of the morphs vary geographically (Creed, 1975). Females of this species have shown a preference to mate with the rare male morph in the population both in field and laboratory conditions (Muggleton, 1979; Majerus, O'Donald & Weir, 1982).

Another invertebrate species in which a rare male effect has been found is the African monarch butterfly *Danaus crhyssipus*, which presents a colour polymorphism with two common morphs that have either nut-brown or orange wings. Smith (1975) observed in wild populations that the orange male morph had a mating advantage lasting 3 to 4 months, which was lost as its frequency increased. The mating advantage of both morphs fluctuated through the duration of the study (26 months) with each morph being favoured when rare; however, density-dependent selection could not be ruled out as an explanation for the observed polymorphism, because density and frequency covaried in the study population (Smith, 1975), and density-dependent selection is another mechanism that can potentially maintain genetic polymorphisms (Roughgarden, 1971; Moorcroft *et al.*, 1996; Sinervo, Svensson & Comendant, 2000).

Although the rare male effect is quite well supported in some systems, just as in other scenarios in which NFDS generated by sexual interactions might explain the continued persistence of polymorphism, frequency-independent abiotic factors have also been implicated. In several *Drosophila* species, there is clinal variation in pigmentation correlated with latitude, altitude, humidity and temperature (Hollocher, Hatcher & Dyreson, 2000; Brisson *et al.*, 2005; Pool & Aquadro, 2007; Rajpurohit, Parkash & Ramniwas, 2008; Parkash *et al.*, 2011). A similar correlation has also been found in the ladybird *Adalia bipunctata*, and the variation in colour observed has been suggested to be a result of gene flow among populations experiencing different selection on melanization for thermoregulation (Brakefield, 1984; de Jong & Brakefield, 1998). Additionally, as pointed out by Partridge (1988), for the rare male effect to account for genetic diversity in natural populations, female mating preferences should act on phenotypic variability at all polymorphic loci.

## Male–male interactions

When individuals in a population are competing for the same resources, genetically determined alternative strategies to exploit those resources can arise. In nature, males of different species have been observed to adopt alternative mating strategies when competing for females (Gross, 1985, 1991; Maekawa & Onozato, 1986; Shuster & Wade, 1991; Bleay *et al.*, 2007). Theoretically, these alternative strategies can be maintained by NFDS when an individual's fitness is affected by the frequencies of neighbouring morphs with which it is competing in its social environment (Gadgil, 1972; Maynard Smith, 1982; Sinervo & Lively, 1996). In invertebrates, the only species where alternative strategies that are known to be genetic in origin have been observed is the marine isopod *Paracerceis sculpta*. However, the polymorphism does not involve colouration, and no formal test of NFDS has been made (Shuster & Wade, 1991).

Genetically determined alternative male mating strategies have been more widely studied in vertebrates, predominantly in birds, fish and lizards (Gross, 1985; Maekawa & Onozato, 1986; Sinervo & Lively, 1996; Tuttle, 2003; Bleay *et al.*, 2007; Formica & Tuttle, 2009). Nevertheless, examples providing

evidence for NFDS as a mechanism for their maintenance are scarce, and most are of behavioural polymorphisms that are not associated with colour (Gross, 1985, 1991). The only study that evaluates NFDS in the maintenance of alternative male mating strategies associated with colour is in the side-blotched lizard *Uta stansburiana* where males show three different throat colours. Male morph frequencies have been observed to oscillate in a manner consistent with NFDS in natural populations (Sinervo & Lively, 1996), and it has been empirically demonstrated, by manipulating morph frequencies in the field, that a particular morph has a higher mating success when it is rare relative to its antagonistic morph (Bleay *et al.*, 2007). However, even in this well-studied example, some doubt remains about the importance of NFDS, since not all the variance in morph fitness over time and space is satisfactorily explained by frequency (Bleay *et al.*, 2007). Interestingly, evidence for a mechanism analogous to heterozygote advantage (a two-locus mode of inheritance with recessive epistasis) in the maintenance of colour polymorphisms has been found in females of other species of lizards with alternative reproductive strategies (Calsbeek, Bonvini & Cox, 2009; Vercken, Clobert & Sinervo, 2010), highlighting the potential role for other mechanisms in such cases.

## Effects of predators on prey

Interactions between predators and prey have been the focus of many studies of conspicuous polymorphisms. It has long been thought that prey colouration may reflect an evolutionary response to the foraging strategies and cognitive characteristics of predators. Clarke (1962a) proposed a negative frequency-dependent mechanism, involving differential predation of various prey types, which was able to account for conspicuous polymorphisms. He termed this mechanism apostatic selection. He hypothesized that if a predator consumes disproportionately more of a common prey type because it encounters it more frequently, and overlooks a rare type, then the frequency of the common type will decrease, and the frequency of the rare type will increase. Eventually, a point will be reached at which the once rare prey type is the more common of the two, and the predator will start to consume disproportionately more of this type. Intuitively, the long-term consequence of such negatively frequency-dependent behaviour by the predator will be the stable coexistence of the two prey types. Clarke's hypothesis was given weight by his studies of two polymorphic snail species of the genus *Cepaea*, *C. nemoralis* and *C. hortensis*, in which he provided evidence consistent with frequency-dependent predation of the morphs by the song thrush *Turdus philomelos* (Clarke, 1962b).

Apostatic selection is generated by a pattern of prey consumption that can be characterized by a sigmoid or 'Type III' functional response (Holling, 1965). Such a response by predators to changing prey frequency is thought to arise from the presence in the predator of a 'search image', which results in prey 'switching'. Switching, in the general sense, refers to the tendency of predators to change food sources as their frequencies vary, focusing on the most abundant prey type available, but switching to an alternative type when it becomes

relatively more common (Murdoch, 1969). The idea of the search image was proposed by Tinbergen (1960) after observing the patterns of insectivorous birds preying on different species of cryptic caterpillars on pine trees. In Tinbergen's study, the birds showed a frequency-dependent consumption of caterpillars, as well as a delay of two to three days for the incorporation of new species in their diet. Tinbergen hypothesized that the birds needed a certain number of chance encounters with novel prey to be able to form a search image for them. Inherent in this idea was the concept that detection of prey represents a sensory 'problem', and hence the search image is typically considered only to facilitate prey detection when prey are cryptic (Tinbergen, 1960; Dawkins, 1971; Lawrence & Allen, 1983; Dukas, 2002). It has been demonstrated that the formation of a search image is a result of selective attention after a sequential exposure to a particular stimulus (Croze, 1970; Bond & Riley, 1991; Blough, 1992; Reid & Shettleworth, 1992; Langley, 1996; Bond & Kamil, 1999; Dukas & Kamil, 2001). A predator forming a search image will focus on certain features of a frequently encountered prey type that enable it to detect the prey more efficiently, but this focus will interfere with the detection of other types of prey that lack the appropriate features (Kamil & Bond, 2006). When the more common prey type becomes rare, 'perceptual switching' is predicted to occur (Bond, 2007) as a new search image is formed after a series of consecutive detections of what is now the most abundant prey type. This change in search image is what produces the actual switch in predation levels on different prey types.

Apostatic selection has primarily been studied in the context of colour polymorphisms in invertebrates, where the main agent of selection has been assumed to be predation by birds. The fact that birds are easily trained to perform specific tasks in experimental conditions, and that they prey upon colour-polymorphic invertebrates with low mobility (e.g. snails), facilitates the study of patterns that are consistent with apostatic selection. In order to demonstrate that apostatic selection occurs, and is capable of maintaining balanced polymorphisms, it is first necessary to establish that predators that feed on polymorphic prey show perceptual switching. This has been demonstrated in laboratory free-choice experiments such as the one carried out by Bond (1983), in which he presented different types of grain on two kinds of background where they were either cryptic or conspicuous to pigeons. The pigeons showed a preference for the more common grain on the cryptic background. The effect was lost when the grains were conspicuous. The response rate was reduced as the relative proportions of grain types became equal, which Bond explained could indicate a decrease in searching efficiency owing to repeated switching from one grain type to another. Other laboratory free-choice experiments have supported the occurrence of perceptual switching (Cooper, 1984; Tucker, 1991; Reid & Shettleworth, 1992; Cooper & Allen, 1994). Operant conditioning studies have also demonstrated that if a bird experiences sequential presentations of the same prey type, it will detect that prey type more efficiently over time; in contrast, there will be a reduction in the efficiency of detection when presented with a novel prey type or a sequence of mixed

prey types (Blough, 1989; Langley, 1996; Bond & Kamil, 1999). In more realistic conditions, wild birds presented with different artificial prey at varying frequencies in natural surroundings have been shown to attack the more common prey type disproportionately, with this effect being stronger on more complex backgrounds and at low prey densities (Allen, 1972; Allen, 1976; Cooper, 1984). Similar results have been obtained from experiments with natural prey in semi-natural conditions, using fish (Murdoch, Avery & Smyth, 1975; Maskell *et al.*, 1977; Jormalainen, Merilaita & Tuomi, 1995) and birds (Allen, 1988; Tucker, 1991).

It has thus been demonstrated, in laboratory conditions, that vertebrate predators will disproportionately attack prey they encounter more frequently, and that prey switching can happen as a result of the formation of a search image. This, however, does not prove that natural polymorphisms are maintained through apostatic selection. It is necessary to test for the long-term coexistence of prey morphs and dynamics in morph frequencies over time that are consistent with the predicted effects of perceptual switching. Using a 'virtual ecology' approach, Bond & Kamil (1998, 2002) not only showed that apostatic selection happens, but also that it can also promote phenotypic diversity. They created a digital moth population modelled on the genus *Catocala* with three discrete morphs in equal numbers and exposed them to predation by blue jays, *Cyanocitta cristata*. After 50 generations, the frequencies of all three morphs reached an oscillatory equilibrium that was independent of their initial numbers, and was maintained by apostatic selection alone. To test if apostatic selection could also promote phenotypic diversity, digital moth phenotypes were specified by genomes that were subject to mutation in each generation, starting with a monomorphic population. Experimental lineages were compared with two control lineages: one that was left to evolve by drift alone, and a second one that was under frequency-independent directional selection for crypsis. In both the experimental line and the frequency-independent control, moths developed a higher level of crypsis. However, only in the frequency-dependent line was an increase in phenotypic diversity observed.

Although perceptual switching, which is proposed to occur only when prey are cryptic, is the most common mechanism used to explain apostatic selection, there is evidence for apostatic selection from experiments with predators attacking non-cryptic prey (Manly, Miller & Cook, 1972; Harvey, Jordan & Allen, 1974; Cook & Miller, 1977; Willis *et al.*, 1980; Greenwood, Wood & Batchelor, 1981). In these examples, alternative behavioural mechanisms may be the proximate causes of apostatic selection. For example, previous experience with a frequently encountered prey type can lead to the modification of search tactics, improvement in handling efficiency, and/or learning of specialized hunting techniques (Dawkins, 1971; Krebs, 1973; Murdoch *et al.*, 1975). Nevertheless, there is little direct evidence supporting these mechanisms as causes of apostatic selection (Bergelson, 1985; Cothran & Thorp, 1985; Elliott, 2006). The disproportional consumption of a common prey morph by predators can also be a consequence of the avoidance or preference of a particular prey that is independent of the predator's ability to detect,

handle or attack the different morphs (Krebs, 1973). This preference might result from dietary wariness, a mechanism that involves an initial temporary reluctance to try novel prey (neophobia) and a latency to incorporate the prey into the normal diet (dietary conservatism) (Marples & Kelly, 1999; Mappes, Marples & Endler, 2005; Marples *et al.*, 2007). Computer simulations have demonstrated that the effect of dietary wariness is powerful enough to maintain polymorphisms in both cryptic and non-cryptic prey, and it can be a more important mechanism producing apostatic selection than attentional mechanisms (Franks & Oxford, 2009, 2011).

Despite the effects of dietary wariness shown by computer simulations, and Bond & Kamil's (1998, 2002) elegant demonstration of the potential for apostatic selection via search image formation to promote polymorphism, equivalent data from natural populations of prey are lacking. As a result, while apostatic selection is often identified as the most plausible explanation for observed conspicuous polymorphisms in invertebrates, we have little direct support for this view. There are only a couple of studies in natural populations that in fact test for apostatic selection, both on the mangrove snail *Littoraria filosa*. Reid (1987) manipulated the morph frequencies of *L. filosa* on individual bushes of *Avicennia eucalyptifolia*, and found that the disappearance of yellow and brown shells was frequency-dependent, each morph being favoured when rare. Reid ruled out the influence of climatic factors because he found no difference in morph frequencies between sunny and shaded trees, or among seasons. Similar results were obtained in more recent experiments with the same species (McKillup & McKillup, 2008), with the disappearance of the different morphs being attributed to predation by crabs. Even though these results show that negative frequency-dependent predation happens in natural populations, they are still not sufficient to conclude that apostatic selection is occurring, because the long-term dynamical consequences of the observed changes in morph frequency in *L. filosa* are not known. Thus, these studies are still a long way from proving that apostatic selection maintains prey polymorphism at equilibrium. Unfortunately, the level of experimental control required makes it very difficult for more definitive experiments to be done with natural populations.

Studies in several species of snails have shown that apostatic selection might not play a central role in the maintenance of polymorphism. For example, the shell colour polymorphism in the marine snails of the genus *Littoraria* has been attributed to adaptation to local environmental conditions and spatially varying selection for the ability to thermoregulate (Merkt & Ellison, 1998; Phifer-Rixey *et al.*, 2008). Similarly, shell colour variation in several species of land snails is thought to be the result of climatic selection (Abdel-Rehim, 1983; Hazel & Johnson, 1990; Slotow & Ward, 1997; Cazzaniga, Piza & Ghezzi, 2005; Johnson, 2011). Even in the land snails of the genus *Cepaea*, which are perhaps the most extensively studied polymorphic taxa, and which inspired early accounts of apostatic selection (Clarke, 1962a), studies have shown that there are frequency-independent mechanisms that are sufficient to explain the colour polymorphism even in the absence of NFDS. These factors include drift, founder

effects and differentiation in refugia leading to area effects, and migration combined with geographically variable selection pressures, such as those associated with climate and predation (Goodhart, 1962, 1963; Cain & Currey, 1963; Carter, 1967; Jones, Leith & Rawlings, 1977; Chang & Emlen, 1993; Wilson, 1996; Cook, 1998, 2005; Cook & Pettitt, 1998; Cowie & Jones, 1998; Davison & Clarke, 2000; Cameron, 2001; Bellido *et al.*, 2002). Although apostatic selection has not been directly tested in natural populations of *Cepaea*, the conclusion that frequency-independent forces are more a plausible explanation for the persistence of the observed polymorphism are based on inconsistencies between morph frequency patterns observed in some areas and those expected if apostatic selection was operating (Cain & Currey, 1963; Carter, 1967; Cook & Pettitt, 1998). The current consensus is, therefore, that apostatic selection is of minor importance in this system.

In summary, empirical work on natural populations does not, as yet, support the idea that apostatic selection plays a major role in the maintenance of polymorphisms. Nevertheless, studies that test for apostatic selection in natural conditions are very scarce. Furthermore, our understanding of apostatic selection comes almost exclusively from studies of vertebrate predators, despite the fact that invertebrates, with very different sensory and nervous systems, may be important agents of selection in some systems. Clearly, more detailed field experiments are required. However, theoretical and some empirical studies have shown that the potency of apostatic selection as a driver of diversity is highly sensitive to variation in ecological factors such as prey and predator densities, dispersal, habitat heterogeneity and the spatial distribution of prey (Greenwood, 1969; Cook & Kenyon, 1991; Allen, Raison & Weale, 1998; Merilaita, Tuomi & Jormalainen, 1999; Weale *et al.*, 2000; Shigemiyama, 2004; Merilaita, 2006; Endler & Rojas, 2009; Merilaita & Ruxton, 2009). The effect of apostatic selection can be weakened or even eliminated if one or more of these factors are manipulated. Consequently, it seems likely that in many systems apostatic selection cannot explain polymorphism on its own.

## Other interactions

### Host–parasite interactions

Interactions between parasites and their hosts can lead to NFDS, and hence have the potential to maintain polymorphisms, although in most examples, these polymorphisms are not apparent to the observer. If some degree of genetic matching is necessary for a parasite to infect a host, then hosts with rare genotypes will suffer fewer infections (Hamilton, 1980; Hamilton, 1993). As the fitness of common hosts decreases, so will their frequency, and the frequency of rare hosts will increase. Following the Red Queen model of co-evolution, parasites will evolve to counteract this adaptation, and, after a certain period, parasite genotypes that are best able to infect the hosts that were initially rare will be selected for (Decaestecker *et al.*, 2007). This will generate an advantage for rare genotypes that could potentially maintain variation in a population (Tellier & Brown, 2007).

While there is some empirical support for the idea that frequency-dependent host–parasite interactions promote cryptic genetic polymorphisms in invertebrates (Dybdahl & Lively, 1998; Lively & Dybdahl, 2000; Decaestecker *et al.*, 2007; Duncan & Little, 2007; Wolinska & Spaak, 2009; King *et al.*, 2011), impacts on conspicuous phenotypes are not well documented. One example providing evidence supporting the effect of parasitism on the maintenance of colour polymorphisms is in the pea aphid *Acyrtosiphon pisum*, where individuals can have either green or red colouration (Langley *et al.*, 2006). The parasitoid wasp *Aphidius ervi* was shown to be more likely to attack aphids of the same colour morph as those they had experienced recently (Langley *et al.*, 2006). A dynamic model showed that this behaviour of *A. ervi* can lead to a preference to parasitize the common colour morph, and is sufficient to explain fluctuations in morph frequencies observed in the field over a period of several years (Langley *et al.*, 2006). NFDS from host–parasite interactions has also been studied in the marine snail *L. filosa*, which shows variation in shell colour. It has been observed that the parasitoid sarcophagid fly *Sarcophaga megafilosa* selects for cypsis in natural populations of *L. filosa* by attacking a higher proportion of snails that do not match their background (McKillup & McKillup, 2002). However, when the frequencies of *L. filosa* morphs were manipulated, *S. megafilosa* showed a bias for a particular morph when it was rare (McKillup & McKillup, 2008). This pattern would produce positive frequency-dependent selection and thus would more likely lead to the fixation of the common morph than the persistence of the polymorphism. In the absence of any other published examples of this sort, we therefore conclude that, while it is technically possible that frequency-dependent fitness effects of parasites might maintain conspicuous polymorphisms in their hosts, no strong evidence exists that this is the case.

### Effects of prey on predators

Studies of predator–prey interactions leading to NFDS have focused almost exclusively on the effect that predators have on prey populations (see earlier). The possibility of prey affecting the frequencies of morphs in predator populations has received far less consideration. If a predator's main prey can discriminate between predator morphs, it might learn to avoid the predator morph that it encounters more frequently by associating it with a potential attack. Predators of the morph that is avoided by prey are expected to catch fewer prey and feed less often, which will affect their fitness and cause their frequency to decrease relative to rare morphs that are not as easily recognized by the prey. Such frequency dependence could maintain a balanced polymorphism in exactly the same way as was originally predicted when predators forage preferentially for common prey morphs.

Evidence for NFDS on predator morphs by prey is scant (Hori, 1993), but there is clear potential in some systems. For example, some spiders show conspicuous variation in body colour and pattern (Théry & Casas, 2009), and attack prey, such as bees, which are known to be able to discriminate colours (Giurfa, 2004; Dyer & Neumeyer, 2005; Srinivasan,

2010; Dyer, Paulk & Reser, 2011). Studies have shown that spider colouration affects the behaviour of some prey species in such a way that spider fitness is likely to be affected (Hauber, 2002; Tso, Lin & Yang, 2004; Heiling *et al.*, 2005; Tso *et al.*, 2006; Ings & Chittka, 2008; Herberstein, Heiling & Cheng, 2009; Llandres *et al.*, 2011). Most studies that have investigated colour variation in spiders have concentrated on species with forms that choose their backgrounds in relation to their colour, and use colouration to appear cryptic or to attract prey (Théry & Casas, 2002; Heiling, Herberstein & Chittka, 2003; Heiling *et al.*, 2005; Defrize, Théry & Casas, 2010). However, we have found evidence in favour of prey avoiding recently encountered colour morphs of the crab spider, *Synema globosum* (H. Ajuria-Ibarra & T. Reader, unpubl. data). This species shows a female-limited colour polymorphism, where females can have red, yellow or white colouration on their abdomen (Roberts, 1995). *Synema globosum*'s main prey are honeybees (*Apis mellifera*), and the spiders appear to choose flowers independently of their colour. We observed that after previously experiencing a simulated attack while visiting a flower harbouring a spider of one morph, honeybees were significantly less likely to visit a flower with a spider of the same morph a second time, whereas no such effect was found if the second flower harboured a spider of a different morph. These results support the idea that a prey's response to a predator's colour morphs could generate NFDS, and could be investigated further to look for evidence that such selection is important in the maintenance of predator polymorphism.

### Conclusion

Even though our knowledge of how NFDS might operate to maintain conspicuous polymorphisms has increased substantially since Fisher (1930), definite evidence supporting its occurrence in natural populations is yet to be obtained. This clearly reflects the difficulty in performing the necessary experiments in natural conditions, but it is probably also partly explained by the fact that real patterns of selection in polymorphic populations are rather more complicated than the simple ecological scenarios envisaged by early proponents of NFDS as a diversifying force (Clarke, 1962a). One reason for this is that frequency often correlates with other explanatory variables in the field, such as sex ratio (Hammers & Van Gossum, 2008) and density (Smith, 1975), which makes it difficult to distinguish between NFDS hypotheses without experimental manipulation of morph frequencies. Additionally, it is important to determine if the observed polymorphisms are genetic in origin. If this is not the case, then frequency-dependent selection cannot account for observed phenotypic variation. However, in polymorphisms that are genetic and in the invertebrates in particular, NFDS generated by different ecological interactions remains one of the most commonly cited explanations for the persistence of colour variation. Unfortunately, in many cases, formal tests of NFDS have not been performed, or have been performed only in the laboratory, and the few experimental studies in natural populations have provided at best partial evidence that NFDS



is operating to maintain variation. The evidence we do have, however, has helped us to understand the many frequency-dependent ways in which conspicuous variation in morphology can affect fitness.

Studies of colour polymorphisms in natural populations of invertebrates have also been important in demonstrating the relevance of alternative mechanisms for the maintenance of phenotypic and genetic diversity. The best examples to date are the extensively studied colour polymorphisms of the land snails in the genus *Cepaea*, where adaptation to local climatic conditions, founder effects and migration have all been shown to be important in explaining the observed phenotypic diversity, and NFDS appears to have only a minor effect. The key feature of the *Cepaea* research is the consideration of multiple mechanisms simultaneously in both empirical and theoretical contexts. In the absence of such detailed studies of other systems, it remains to be seen if the conclusion reached regarding colour variation in *Cepaea* is more widely applicable. In some other systems, such as the sex-limited polymorphisms in damselflies, our understanding of the factors influencing morph frequencies has improved markedly in recent years, but the focus remains mainly on NFDS. In such cases, we need clear theoretical predictions of the patterns, which should arise from the different potential diversifying mechanisms and empirical studies of natural populations that distinguish among these patterns, before we can establish the true importance of NFDS. At least in the case of sex-limited polymorphisms in damselflies, the signs are good: recent modelling (Van Gossum & Sherratt, 2008) and field studies (Iserbyt *et al.*, 2010, 2012; Gosden *et al.*, 2011; Sánchez-Guillén *et al.*, 2011), taking into account the importance of other mechanisms such as genetic drift and gene flow among populations are important steps towards a more complete understanding of the factors promoting the persistence of visible polymorphisms. Whatever future studies of this kind reveal about the contribution of alternative mechanisms to the maintenance of morphological diversity, however, it seems likely that NFDS will continue to be viewed as one of the most plausible and potentially potent forms of selection influencing polymorphisms in natural populations.

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