The co-evolution of anti-predator polymorphisms in sympatric populations

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**Abstract**

Anti-predator defences are varied and widespread in nature. One little-studied form of anti-predator defence involves exuberant visible polymorphisms, where high numbers of morphs are present within a population. We present a model to explore the impact of indirect interactions, via common predators, between sympatric populations of two prey species that share similar morphs. We show that negative frequency-dependent selection by predators leads to a greater divergence of morph frequencies between populations in sympatry than in allopatry. Thus, in sympatry, a morph that is common in one species tends to be rare in the other. We further parameterise the model to approximate thrushes predating populations of the visibly polymorphic land snails *Cepaea nemoralis* and *C. hortensis,* the classical system that first prompted Bryan Clarke to suggest that sight-hunting predators can produce divergence of morph frequencies in sympatry. Our general results suggest that variation in predator ranges over different prey populations is likely to have implications for a number of anti-predator traits.

**Keywords:** anti-predator traits - apostatic selection - avoiding attack - *Cepaea* - crypsis - dietary wariness - polymorphism

1. **Introduction**

Interactions between species can generate selective pressures that lead to reciprocal shifts in characteristics over evolutionary time, an idea that was crystallised in seminal papers by Grant (1949) and Ehrlich & Raven (1964). This co-evolutionary process is now recognized as occurring at both inter- and intra-specific levels (Carmona, Fitzpatrick & Johnson, 2015). The role of co-evolution as a potential promoter of diversity and a driver of speciation has received much attention, mostly involving predator/prey, parasite/host and mutualistic relationships (Yoder & Nuismer, 2010). Many of these studies have involved evolutionary interactions between pairs of species, for example a parasite and its host (Bérénos, Wegner & Schmid-Hempel, 2011) or a plant and its pollinator (Anderson & Johnson, 2008). In the case of both Batesian and Müllerian mimicry, the co-evolution in coloration between model and mimic species is driven by a third species – their mutual predator(s) (Rowe, 2013). However, little attention has been paid to the levels of diversity maintained in non-mimetic situations where two species co-evolve anti-predator adaptations as a result of shared predators.

Anti-predator defences are varied and widespread. Research in this area typically focuses on crypsis, secondary defences such as spines and toxins, or mimicry (Ruxton, Sherratt & Speed, 2004; Mappes, Marples & Endler, 2005; Sherratt, 2008; Stevens & Merilaita, 2011). A less obvious form of anti-predator defence comes in the form of massive or exuberant visible polymorphisms exhibited, for example, by the meadow spittlebug, *Philaenus spumarius* (Halkka & Halkka, 1990) and the spiders *Theridion grallator* (Oxford & Gillespie, 2001) and *T. californicum* (Oxford, 2009). These colour and pattern polymorphisms in undefended prey tend to reduce the *per capita* rate of predation on novel morphs. They do so by increasing the educational burden on the predator in learning to attack the prey as a result of the high number of novel morphs the predator needs to learn (Moment, 1962; Franks & Oxford, 2009; Karpestam, Merilaita & Forsman, 2014; Karpestam, Merilaita & Forsman, 2016). This is in contrast to Müllerian mimicry between defended species and monomorphism within a species of equally defended individuals, both of which serve to decrease the educational burden on the predator in learning to avoid the prey (Mallet & Singer, 1987; Franks & Sherratt, 2007; Sherratt, 2008). Whereas unpalatable species benefit from sharing an appearance through Müllerian mimicry, the opposite is true for palatable prey, which benefit from evolving distinct appearances that slow the speed that predators learn to attack them.

Understanding the mechanisms by which discrete/distinct morph appearances evolve and are maintained in populations forms a major theme in evolutionary biology (Clarke, 1979; Oxford & Gillespie, 1998; Ibarra & Reader, 2013). One process that can maintain multiple morphs is negative frequency-dependent selection, where a morph or an allele is advantageous when rare but disadvantageous when common. The first discussion of negative frequency-dependent selection (although not expressed in this way) exerted by predators was apparently by Poulton (1884), a reference brought to light by Allen and Clarke (1984). However, it was Clarke (1962) who promoted, independently, the notion that the searching behaviour of predators could impose negative frequency-dependent selection on visible traits of a prey species, in a process he called apostatic selection. The hypothesis is that predators become accustomed to looking for common prey morphs having certain visible characteristics and, as a result, tend to ignore rarer morphs exhibiting other visible traits (Tinbergen, 1960; Bond, 2007). In a simple two-morph scenario, the rarer morph is under-predated and has a selective advantage whereas the commoner morph is over-predated and suffers a selective disadvantage. Crucially, as the morphs change in frequency as a result of this selection, the search image used by the predator also changes such that the new, commoner morph is now the one over-predated. The result is that both morphs can be maintained within the prey population; a situation than can easily be extended to the maintenance of several morphs (Bond, 2007).

Clarke (1962) further suggested that, as a result of apostatic selection, there should be indirect interactions – *via* common predators – between sympatric populations of species that share similar morphs. While much work has focussed on demonstrating apostatic selection, both in the laboratory and in the field, and its potential role in promoting polymorphism (Allen & Clarke, 1984; Sherratt & Harvey, 1993; Ibarra & Reader, 2013) the second aspect of Clarke’s argument regarding the interaction of prey species has largely been overlooked.

Clarke’s proposition was that in sympatric populations, apostatic selection acting on similar visible morphs shared by two prey species should lead to a divergence of morph frequencies between them. Thus, a morph that is common in one species should be rare in the other. In this respect, the populations of the two species co-evolve genetic variation as a result of co-predation. On the other hand, in isolated populations of the two species that lack shared predators, there would be no selection for inter-specific morph divergence, assuming that morphs are equal in all respects other than appearance. Samples of the highly visibly polymorphic landsnails *Cepaea* *nemoralis* and *C. hortensis* collected from sympatric colonies within sixty miles of Oxford appeared to support his prediction (Clarke, 1962). However, Carter (1967) criticised Clarke’s suggestion that the divergence of morph frequencies in the two species was a result of apostatic selection and he failed to detect any consistent morph-frequency associations in additional sympatric populations. Clarke (1969) rebutted these conclusions and showed that further analysis of Carter’s data did indeed show divergence of morph frequencies in most of the sympatric populations studied. To our knowledge, the effect of apostatic selection on morph frequencies in sympatric populations has not been investigated since, either theoretically or using field data. If recognizable patterns in morph frequencies between sympatric and allopatric populations as a result of joint predation can be verified and quantified, they may serve as indicators of negative frequency-dependent selection under natural conditions.

We have previously considered the individual and combined effects of apostatic selection and dietary wariness on the evolution of exuberant visible polymorphisms within single populations (Franks & Oxford, 2009; Franks & Oxford, 2011). Dietary wariness comprises two behavioural processes; neophobia and dietary conservatism (Marples & Kelly, 1999). Neophobia is the initial avoidance of a novel food item and is usually short-lived. Once accepted as food, dietary conservatism describes a longer-term reluctance to incorporate fully the food item into the predator’s regular diet (Marples, Roper & Harper, 1998; Marples & Kelly, 1999). Both apostatic selection and dietary wariness lead to negative frequency-dependent selection. However, in the case of dietary wariness once a reluctance to eat a novel prey morph is overcome that morph ceases to have a selective advantage over other morphs for the rest of an individual predator’s lifespan. In contrast, in apostatic selection, a morph can move from being advantageous to being disadvantageous, and back again, according to its relative frequency and concomitant shifting search images within a predator’s lifetime. We found that both mechanisms produce polymorphisms, with dietary wariness (conservatively implemented as neophobia alone – see below) having the strongest effect. Although Clarke (1962) invoked apostatic selection as the mechanism driving negative frequency-dependent selection, we have additionally applied dietary wariness as a potential alternative mechanism.

Here we explore the effect of predators preying on both isolated (allopatric) and mixed (sympatric) populations of two species with the potential for shared morphs. This allows us to test quantitatively for the first time Clarke’s (1962) prediction of a co-evolutionary divergence in the frequencies of identical morphs in sympatric prey populations with apostatic selection, dietary wariness and combined models. We also explore a model parameterised to reflect the *Cepaea* snail and thrush situation that stimulated Clarke’s ideas.

1. **Methods**

We modify our established individual-based model of apostatic selection and dietary wariness (Franks & Oxford, 2009) based on a previous model of apostatic selection (Merilaita, 2006). The purpose of the model is to compare evolution in sympatric and allopatric prey populations. Thus, we assume the existence of a learning predator in each case, and treat the allopatric scenario as the null situation. Prey individuals are haploid and all morphs are determined by alleles at a single locus and are equally visible and palatable to predators. We assume that all individuals are similar in all respects other than appearance (e.g. in resource value, growth rate and protective strategy).

The model begins with *m1* individuals of one species, *m*2 individuals of the other, and *n* predators. At every time-step, *t*, each predator is presented with individual prey items, randomly drawn with replacement from the surviving individuals of both populations, until it detects one (or unless there are no prey items left to present). The order of individual predators to be presented with prey is shuffled in every time-step. Each predator has its own detection probability for each morph *i,* given by *P*(*i*)t. Under apostatic selection a predator improves its ability to detect a commonly encountered morph while simultaneously reducing its probability of detecting rarely encountered morphs. If a predator detects morph *i* at time *t*, then , while for all *j* morphs given *j* ≠ *i* (regardless of whether morph *j* has yet been encountered). The level of adjustment *δ* defines the strength of apostatic selection. We use two values, *δ =* 0 (no apostatic selection) and *δ =* 0.1 (a high level of apostatic selection). These adjustments act within set limits of detection *P*(*j*)*min* ≤ *P*(*j*) ≤ *P*(*j*)*max*. We set the initial detection probability *P*1 = 0.3, with limits *P*min = 0.2, *P*max = 0.8. The limits allow us to keep the values within bounds and prevent prey becoming invisible. We assume that the memory of past predation events are not forgotten.

We introduce dietary wariness in our model by assuming that predators always avoid the first prey individual they experience (encounter and detect) of a novel morph, which is a conservative implementation of just the neophobic element of dietary wariness (Marples & Mappes, 2011). Once overcome, dietary wariness remains at zero for the rest of the predator’s lifetime. Justification and exploration of parameters can be found in (Franks & Oxford, 2009).

A prey generation comes to an end when less than 50% of either prey population remains (note that this modelled predation pressure does not necessarily correspond to natural levels). The surviving prey then reproduce asexually and at random from the survivors in their own population until each is restored to *m1* and *m2* individuals, and the next time-step (and prey generation) begins. During the reproductive process offspring mutate to a different morph with probability 0.0005, a figure that reflects both actual mutation and the introduction of alleles from other populations *via* rare migration events. The mutation operator works by mutating the individual’s current morph to any of the morphs with equal probability.

We represent the number of possible alternative distinctive morphs – one of which a prey individual can express – by *d,* set to 30 for this study. We are simulating haploid organisms and thus have direct counts of allele frequencies. In our simulations when counting the number of morphs, we include only those morphs comprising ≥ 1% of the population. At the start of each simulation the prey of both species are fixed for the same random morph.

We set the number of predators *n* = 80, and the number of individuals in each population to *m*1 = 400, *m*2 = 400. We reset the attack probabilities of predators to their initial state after *g* prey generations, so *g* is the relative lifespan of the predator in prey-life-span units. Thus, the lower the value of *g*, the more often predators will be naïve. We used *g* = 5. We ran 50 model replications for each condition, for 105 prey generations, which was more than enough time for the system to reach a steady state with a constant turnover of morphs, but with little change in the number of morphs.

We ran an allopatric model as specified above with predators only predating one species (half on each); equivalent to predation on two allopatric populations. Our sympatric model involved predators forage in a single, sympatric population irrespective of species identity. We also explored the effects of varying parameter values for *d, n* and *g* (online supporting information). Altering parameter values for *d, n* and *g* make very little difference to our general conclusions (Figures A1 to A3, appendix). In addition, we ran the model applying both apostatic selection and dietary wariness at the same time (Figure A4, appendix).

We used a measure *OAB* to quantify an overlap in morph proportions; the degree to which species *A* and species *B* share morphs. This was defined as:

Where *PA,i* is the proportion of individuals in species *A* that are of morph *i*. The higher the overlap, the more the two species share the same morphs and at similar proportions. When *OAB* is 1, the species share the maximum overlap, and when it is zero, they do not overlap at all.

Finally, we ran the model with parameters representing, approximately, the *Cepaea nemoralis*/*C. hortensis* (prey) and thrush *Turdus philomelos* (predator) system studied by Clarke (1962). Here the prey species live for approximately four to six years (Cain, Cook & Currey, 1990) while the predator’s life-span is about half of this (British Trust for Ornithology, 2017). It is assumed that the prey population lies within the territory of five thrushes (*n* = 5) predating under dietary wariness. Under this scenario predators were replaced with naïve individuals twice per prey generation (g = 0.5). Predators turn over at 90% and 80% of remaining prey and the prey populations are replaced when < 80% of one or other species remains. The number of possible visible morphs was limited to d=6, i.e. three shell colours (yellow, pink and brown) x two banding morphs (5-banded and effectively unbanded) (Cook, 2017). We ran the *Cepaea* version with dietary wariness alone. All other parameter values were as previously stated. We also investigated the number of generations required for the allele frequency differences between prey species in sympatry to maximise under these conditions.

1. **Results**

We first examined the number of morphs evolving in each prey population for both the allopatric model (distinct predators for each prey species) and the sympatric model (shared predators).

Figures 1a and 1b summarise the results for apostatic selection. The total number of morphs evolving across both species is significantly higher in allopatric than in sympatric populations (Wilcoxon rank sum test: n=50, w = 2116, p < 0.01), and the number of morphs present within a species is also significantly higher in allopatry than sympatry (Wilcoxon rank sum test: n=50, w = 9417, p < 0.01; performed on the combined values for species A and B). The median numbers of equally visible morphs maintained in each of the allopatric populations is 9.4 (when the maximum number of morphs available is 30) with the total morphs across both populations 15.7, implying some shared morphs between the two species under the allopatric scenario. Thus, some of the morphs maintained have, by chance, arisen independently in the two populations. In contrast, in sympatric populations the number of morphs maintained per species is lower (7.0 morphs) and the total morphs across both populations is close to 14 (13.6), implying that distinct morphs have evolved in the two species as a result of shared predators.

We also examined variations of these simulations where predators exhibited only dietary wariness (Figure 1c; 1d). We found the same qualitative results, but with a stronger effect from dietary wariness in the number of morphs that evolve. The key result is that the number of morphs within a species is, as before, significantly lower in sympatry than allopatry (Wilcoxon rank sum test: n=50, w = 9997, p < 0.001; performed on the combined values for species A and B). In allopatry the median numbers of morphs maintained within species is now 20.0 and the median total number of morphs across both species is close to the maximum at 26.9. In sympatry, the median total number of morphs within species is 14.7 and the total across species, 29.0. The total number of morphs evolving across both species is significantly different between allopatry and sympatry (Wilcoxon rank sum test: w = 266, p < 0.01).

Applying our measure of morph-frequency overlap (*OAB*), we show this is much higher in allopatry than in sympatry (Wilcoxon rank sum test: n=50, w = 2051.5, p < 0.001; for the apostatic treatment; w = 2500, p < 0.001 for the dietary wariness treatment – Figure 2)

This further demonstrates that sympatry leads to selection for the divergence of morphs and their frequencies between prey species, resulting from shared predation. In contrast, in allopatry there are no common predators and thus the prey species are independent and share morphs by chance.

Finally we modelled an approximation of the snail and thrush situation under a regime of dietary wariness. In this scenario, rather than start from monomorphism, we initialised the model with individuals shared equally between all morphs within each species. Despite many fewer morphs the number that evolved within species was significantly lower for the sympatric simulations than for the allopatric case (Figure 3) (Wilcoxon rank sum test: n=50, w = 2100, p < 0.001). Figure 4 shows that, as in the general scenario, the level of overlap in morph frequencies is also significantly lower in sympatry (Wilcoxon rank sum test: n=50, w = 2100, p < 0.001). To estimate the time needed to generate divergence in morph-frequency overlap we average across 20 sympatric simulations the number of prey generations until divergence stabilised. Figure A5 shows that it takes about 1360 prey generations before the level of overlap reaches a steady state of 0.32 (the mean overlap from generation 2000 onwards).

1. **Discussion**

Our model shows that negative frequency-dependent selection by predators leads to a greater divergence of morph frequencies between populations in sympatry (shared predators) than in allopatry. Thus, in sympatry, a morph that is common in one species tends to be rare in the other, implying that a morph that occurs and spreads in one species precludes the establishment of the same morph in the other species, should it arise *via* mutation or migration. In allopatry, on the other hand, the total number of morphs is lower than the sum across the separate species, showing that the species share some morphs that have, by chance, arisen independently within them.

This is supported by our measure of morph-frequency overlap (*OAB*), where in sympatry there is close to no overlap. In contrast, in allopatry there are no constraints on the morph or its frequency that can arise because there are no interactions between species, and the overlap value is significantly higher. Thus, the indirect evolutionary influence of one prey species on the other *via* shared predators results in morphs that are common in one species being rare in the other.

Our model offers a theoretical underpinning to Clarke’s (1962) verbal prediction that there will be strong interactions between sympatric populations of similar species that have shared visible polymorphisms and which are exploited by common predators. During the evolution of this system there will, necessarily, be a negative association between morph frequencies in the two sympatric species, as Clarke supposed (Clarke, 1962).

In previous simulations involving these two negative-frequency-dependent processes, we have shown that dietary wariness, despite being implemented in a minimal way (single-experience neophobia), is a much more powerful evolutionary force maintaining variation than apostatic selection, and that dietary wariness totally swamps any influence of apostatic selection when they act together (Franks & Oxford, 2009; Franks & Oxford, 2011). In the simulations presented here, therefore, we have not shown the combined effect of apostatic selection and dietary wariness although these models have been run and confirm that dietary wariness alone produces the same results as a combination of the two mechanisms (Figure A4, appendix).

We also modelled the *Cepaea* snail scenario that stimulated Clarke’s original speculations. Under these conditions, the total numbers of morphs establishing within a species is significantly different between allopatric and sympatric populations but, because of the constraint on the number of morphs, each species still shares around five out of the six morphs in sympatry (compared to sharing all six in allopatry). We recognise that this snail/thrush model is simplistic in that it focuses on predation effects alone and does not incorporate differences in the size, behaviour, physiology or genetic interactions within species (e.g. (Bantock, Bayley & Harvey, 1975; Jones, Leith & Rawlings, 1977), differential visibility of morphs (Surmacki, Ozarowska-Nowicka & Rosin, 2013), selection unrelated to their visible properties (Clarke 1962), or overlapping generations. Given the complicating variables outlined above identifying the outcome of negative frequency-dependent selection on sympatric populations of *Cepaea* species is likely to be difficult. We show in our model that the maximisation of morph-frequency differences in sympatry takes more than 1000 snail generations, which reduces even further the likelihood of detecting differences between allopatric and sympatric populations given the likely instability of habitats and predators over such a period. Although *Cepaea* presents a challenging system in which to look for divergence in sympatric populations, other species pairs with shared morphs e.g. the strictly annual spiders *Enoplognatha ovata* and *E. latimana* (Oxford, 1991; Oxford & Reillo, 1993), might be more tractable.

There is evidence for an adaptive role of polymorphism on individuals and possibly populations (Karpestam et al., 2014; Karpestam et al., 2016) as a result of lower overall prey detection (Dukas & Kamil, 2001; Dukas, 2002). Indeed, search images may have evolved in predators in order to enhance the detectability of visibly polymorphic prey, rather than search images promoting visible polymorphisms in prey species (Karpestam et al., 2014; Karpestam et al., 2016). Here we have demonstrated divergent selection in sympatric populations of two visibly polymorphic species as a result of shared predators imposing negative frequency-dependent selection *via* search-image formation and/or neophobia. The patterns of shared alleles and allele-frequency overlap found when comparing sympatric and allopatric populations would not be expected in the absence of this type of selective force. Thus discovering such patterns in the wild would provide a *prima facia* case for our scenario.

More generally, if the predators are wide ranging they could have similar effects on localised allopatric populations of the species, thus eliminating the allopatric-sympatric distinction we make here. The matter may be complicated further if predators have large overlapping ranges such that a particular prey population shares predators that prey on a different mix of populations (or species) elsewhere. Variation in predator ranges over different prey populations is likely to have implications for a number of anti-predator traits, such as various types of mimicy and warning signal. There is a parallel situation in which prey species are more or less separated in time rather than space (Rothschild, 1963; Huheey, 1980; Speed, 2000) and predators overlap them to varying extents.

**Contributions of Authors**

Both authors jointly conceived of the study, designed the model and drafted the manuscript. DWF implemented the model and performed the analyses with input from GSO.

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**Figure Captions**

**../AnalysisInR/finalFigureMaterials/fig1/Fig1.pdf**

Figure 1: The number of morphs maintained within each species (A and B) and across both combined for sympatric and allopatric populations over 50 replicates each. In (a) and (b) predators exhibit apostatic selection, whereas in (c) and (d) they exhibit dietary wariness. Boxes represent upper and lower quartiles, and whiskers represent the highest and lowest values without the outliers (circles).

**../AnalysisInR/finalFigureMaterials/Fig2new/fig2.pdf**

Figure 2: The morph-frequency overlap (*OAB*) between all morphs in each species, over 50 replicates each. In allopatry the species share more morphs than in sympatry. Boxes represent upper and lower quartiles, and whiskers represent the highest and lowest values without the outliers (circles).

**../AnalysisInR/finalFigureMaterials/fig3new/Fig3.pdf**

Figure 3: Results for the condition representing the snail/thrush scenario detailed in the methods, showing the number of morphs maintained within each species (A and B) and across both combined for sympatric and allopatric populations under a regime of dietary wariness. Results are shown over 50 replicates. Boxes represent upper and lower quartiles, and whiskers represent the highest and lowest values without the outliers (circles).

../AnalysisInR/finalFigureMaterials/fig4/fig4.pdf

Figure 4: The morph-frequency overlap (*OAB*) between all morphs in each species, taken over 50 replications of the snail/thrush model. As before in allopatry the species share more morphs than in sympatry. Boxes represent upper and lower quartiles, and whiskers represent the highest and lowest values without the outliers (circles).