

# THE EVOLUTION OF EXUBERANT VISIBLE POLYMORPHISMS

Daniel W. Franks<sup>1,2</sup> and Geoff S. Oxford<sup>3</sup>

<sup>1</sup>York Centre for Complex Systems Analysis, Department of Biology and Department of Computer Science, University of York, York YO10 5DD United Kingdom

<sup>2</sup>E-mail: df525@york.ac.uk

<sup>3</sup>Department of Biology, University of York, York YO10 5DD, United Kingdom

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Visible genetic polymorphism is a common feature of many species. In most cases, the mechanism(s) underlying the maintenance of such variation remain obscure although apostatic selection has often been suggested. Here, we explore individual-based evolutionary models to understand what features of predator–prey relationships may lead to patterns of exuberant polymorphism similar to those observed in the wild. When all morphs are equally visible, the number of evolved morphs increases with the strength of apostatic selection although even with powerful selection the number morphs is still relatively small. The introduction of dietary wariness increases the number of morphs substantially, even when apostatic selection is absent. When one morph is more cryptic the number of evolved morphs is fewer. The cryptic morph reaches high frequency in the population and other morphs are each at lower frequencies. Decreasing the predation intensity enhances the number of evolved morphs in all models. Dietary wariness is a critical factor missing from earlier models and it may provide a general solution to the problem of polymorphisms involving many morphs. Apostatic selection is shown to be neither a necessary, nor a sufficient, requirement for the maintenance of exuberant polymorphisms.

**KEY WORDS:** Dietary conservatism, massive polymorphism, neophobia, search image, spiders, *Theridion californicum*, *Theridion grallator*.

Genetic polymorphism for pattern and/or color is a common feature of many species, especially invertebrates. The number of morphs can be small, for example in many melanic versus nonmelanic moths (Majerus 1998) and some small mammals (Nachman et al. 2003). In other species, however, the number of discrete forms commonly found within single populations reaches double figures (e.g., in the meadow spittlebug, *Philaenus spumarius*; Halkka and Halkka 1990). These cases, involving tens of color morphs, have been called “exuberant” polymorphisms (Oxford 2009). Although these situations represent arbitrary stages on a continuum of morph numbers, we concentrate here on exuberant polymorphisms because of the challenges they raise with regard to their maintenance. How high levels of genetic variation can be maintained in natural populations has been the subject of consid-

erable interest and debate (Hedrick et al. 1976; Jones et al. 1977; Wright 1978; Hedrick 1986, 2006). One possible mechanism results from the way in which predators locate and attack variable prey. It is often the case that predators over-concentrate on detecting and consuming common prey morphs while under-predating rarer morphs. This form of positive frequency-dependent predation leads to negative frequency-dependent selection in favor of the less common morph(s)—a process known as apostatic selection (Clarke 1962; Allen 1988). Apostatic selection and the relevant underlying cognitive processes of the predator have recently been reviewed by Dukas (2002), Punzalan et al. (2005), Sinervo and Calsbeek (2006), and Bond (2007).

Apostatic selection has been studied in a number of situations ranging from relatively uncontrolled field experiments with

real or artificial prey (e.g., Allen 1976; Reid 1987; Tucker 1991) through laboratory studies using captive predators and real, artificial, or computer-generated (virtual) prey (e.g., Tucker and Allen 1993; Bond and Kamil 1998) to theoretical modeling (e.g., Gendron 1987; Endler 1988; Merilaita 2006). The majority of the experiments investigating the maintenance of polymorphism (or more generally, genetic variation) as a result of predator searching behavior have used a very limited number of prey morphs, often just two.

The present article arose from attempts to understand the adaptive significance of visible genetic polymorphisms in two spider species, the endemic Hawaiian happy-face spider, *Theridion grallator*, and a west coast North American species, *T. californicum*. In both cases, the polymorphism comprises a plain yellow morph at relatively high frequency and a plethora of patterned morphs each, individually, at low frequency (Gillespie and Tabashnik 1989; Gillespie and Oxford 1998; Oxford and Gillespie 2001; Oxford 2009). The genetic control of color in *T. grallator* is well established (Oxford and Gillespie 1996a,b,c); that of *T. californicum* less so (Oxford 2009). Both species live under the leaves of low-growing shrubs and when viewed from beneath, as they would be by a gleaning predator, to human eyes at least the plain yellow morph appears extremely cryptic in the greenish-yellow light filtering through from above. This crypsis, at least in *T. grallator*, is enhanced by individuals remaining immobile and tightly pressed against the leaf surface during daylight hours (Gon 1985, see also Ioannou and Krause 2009). The patterned morphs have opaque patches of red, black, and white superimposed on the yellow opisthosoma (abdomen) that, again to a human observer, make them less cryptic than the plain yellow morph (Oxford and Gillespie 1996a; Oxford 2009; see Stevens and Merilaita 2009). Comparison of levels of population differentiation for color and molecular markers, and morph-frequency changes following natural perturbations, suggest that the color polymorphism in *T. grallator* is maintained by natural selection (Gillespie and Oxford 1998). Color patterns are unlikely to act as intraspecific signals during courtship because species in the family Theridiidae have extremely poor vision (Oxford and Gillespie 2001), and the very nature of the polymorphism together with the spider's behavior (see above) do not suggest aposematism. Gillespie and Oxford (1998; Oxford and Gillespie 1998, 2001) have hypothesized that apostatic selection might be the underlying mechanism maintaining this variation. However, it is not clear whether our current understanding of the mechanisms of apostatic selection can explain the sheer number of morphs involved or the frequency distributions of morphs of varying crypticity.

Experiments by Bond and Kamil (1998), using captive blue jay predating computer-generated "virtual" prey, showed that with three morphs, one more cryptic than the others, the polymorphism was maintained and that in replicate runs the most cryptic form

reached higher frequencies than the less-cryptic forms. In further experiments, the virtual morphs were allowed to evolve with a polygenic model of pattern determination. Here, both the mean level of crypsis and the variance in patterns maintained increased over time (Bond and Kamil 2002). Taken together these results are consistent with apostatic selection, at least under these conditions, being able to maintain and enhance diversity, and produce patterns of morph frequencies such that the most cryptic morph is the most common. Although encouraging, experiments in the laboratory using small numbers of predators do not necessarily reflect the complex conditions experienced in nature. For example, Merilaita (2006) developed an individual-based model and showed that with increasing numbers of predators the power of apostatic selection to maintain polymorphisms decreases.

A factor often invoked as a possible explanation for the evolution of warningly colored patterns in distasteful prey is an initial resistance to accept novel food by a variety of predators (e.g., Marples et al. 1998; Thomas et al. 2003, 2004; Mappes et al. 2005). Mappes et al. (2005) introduced the term "dietary wariness" to describe the combination of a latency to attack a novel food item (neophobia) and a subsequent resistance to incorporate the item into the regular diet (dietary conservatism) (Marples et al. 1998; Marples and Kelly 1999). Neophobia is usually a short-lived aversion whereas dietary conservatism may persist for a very large number of exposures before the novel food is readily eaten. In experiments with wild birds feeding on colored pastry baits, Marples et al. (1998) found that individual European blackbirds (*Turdus merula*) showed a large variation in the number of trials required before they fed regularly on a novel colored bait, ranging from three to well over 100. European robins (*Erithacus rubecula*) under the same conditions took between six and more than 68 trials.

Thomas et al. (2003) conducted experiments with captive European robins predating colored pastry baits in which the frequencies of familiar and novel morphs evolved over trials. They showed that the novel morph reached fixation in more trials than expected by chance alone, as a result of the avoidance of unfamiliar prey (but see Lindström et al. 2001). Thomas et al. (2004) repeated this study in the field, using a number of species of wild bird predators (but mostly robins) and backgrounds on which the familiar baits were more cryptic. The results were similar, with the crypticity of the familiar morph having little effect on the number of times the novel morph reached fixation. Although these authors discussed their data in the light of the origins of aposematic coloration, they did not consider the implications of their work for the evolution and maintenance of visible polymorphisms in palatable species.

Here, we extend Merilaita's (2006) model to explore the evolution and maintenance of exuberant polymorphisms. We simulate the evolution of polymorphism with a high number of possible

morphs of varying crypticity and examine the relative contributions of apostatic selection and dietary wariness to this process.

## Methods

We base our modeling framework on the individual-based, haploid model of Merilaita (2006), but make some significant modifications. The model begins with  $m = 200$  prey individuals, and  $n = 20$  predators. At every time step,  $t$ , each predator is presented with individual prey items, randomly drawn from the population, until it detects one. Each predator has its own detection probability for each morph  $j$ , given by  $P(j)_t$ . All predators begin with  $P(j)_1 = 0.5$ , representing no attack bias or preference for any one morph. The level of adjustment  $\delta$  defines the strength of apostatic selection. A predator improves its ability to detect the prey morphs it feeds on more often, while this simultaneously reduces its probability of detecting the morphs it feeds on less often. If a predator detects morph  $i$  at time  $t$ , then  $P(i)_{t+1} = P(i)_t + \delta$ , whereas  $P(j)_{t+1} = P(j)_t - \delta$  for all  $j$  given  $j \neq i$  (regardless of whether morph  $j$  has yet been encountered). Thus, when  $\delta = 0$  there is no apostatic selection, when  $\delta = 0.1$  there is a high level of apostatic selection. These adjustments act within set limits of detection  $P(j)_{\min} \leq P(j) \leq P(j)_{\max}$ . A prey generation comes to an end when the population reaches  $m/2$  or  $m/4$  individuals (thus varying the intensity of predation on a population). The surviving prey then reproduces asexually and at random from the survivors until the prey population is restored to  $m$  individuals, and the next time-step begins. We end the simulation after a given number of time steps (typically  $10^5$ ).

Our core model deviates from that of Merilaita (2006) as follows:

- (1) At the start of each simulation the prey are monomorphic.
- (2) There are 15 alternative distinctive phenotypes, each of which can be transformed into one of the others by a single mutation.
- (3) At the end of each time period surviving prey are randomly selected to reproduce (rather than surviving prey merely doubling-up) and each offspring mutates to a different morph with probability 0.0005.
- (4) The attack probabilities of predators are reset to their initial state after  $g$  time steps, where  $g$  is the life span of the predator. Thus, the lower the value of  $g$ , the more often predators will be naïve.
- (5) We introduce dietary wariness to predators, where we conservatively assume that predators always avoid the first prey individual they experience (encounter and detect) of a novel morph.

We assume a mutation rate of 0.0005 for each offspring, each time the prey population reproduces. This is high relative to actual mutation rates, but within the term “mutation rate” we also include new alleles replacing old in the focal population as a result

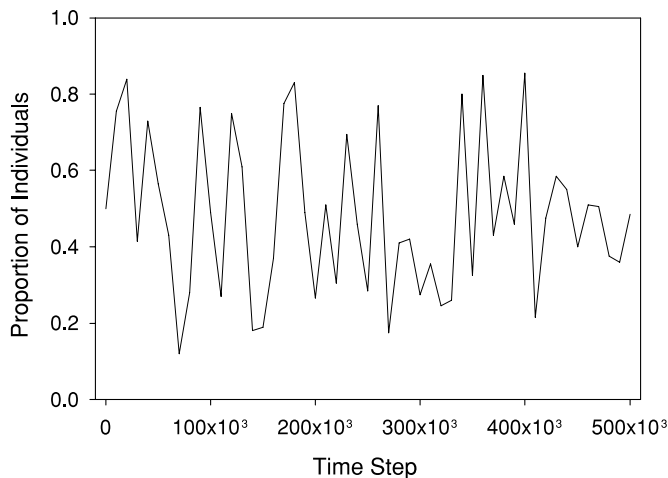
of immigration. We have used adjustment rates of  $\delta$  between zero and 0.1. This range seems reasonable following Bond’s (2007: 500) statement that the number of detections required for the formation of a search image “. . . seems invariably more than one, but generally fewer than five.”

We examine the evolution of polymorphism, from an initially monomorphic population, by allowing up to 15 morphs to evolve. We vary the adjustment rate  $\delta$  to examine the effect of different strengths of frequency-dependent selection on the number of morphs evolved. We vary the number of prey generations that predators live for (predator life span) before their attack probabilities are reset, thus modeling the birth and death of new predators. We are simulating haploid organisms and thus have direct counts of allele frequencies. A commonly used definition of polymorphism is where two or more alleles coexist at frequencies of  $\geq 0.01$  (Hartl and Clarke 2007) which, in a population of  $m = 200$ , translates to two or more individuals. Thus, when counting the number of morphs, we only include those consisting of more than one individual. We have conservatively assumed that dietary wariness for a specific morph, once overcome, remains at zero for the rest of the predator’s lifetime. Likewise, we assume that the memory of past predation events, which results in apostatic selection, is retained from one day to the next.

## Model Exploration

### THE PERSISTENCE OF POLYMORPHISM

Merilaita (2006) showed that a population was polymorphic under frequency-dependent predation only as long as, or for a shorter time than, under frequency-independent predation. Thus, Merilaita concluded that apostatic selection alone is “. . . not a sufficient condition for persistent prey polymorphism.” (2006: 2029). Our replication of the original model—with an initially polymorphic population, no mutation, and two possible morphs—concur with this finding. However, when we extend the model to allow mutation we find different results: even with low levels of apostatic selection polymorphism is persistent. Figure 1 shows an example of a single time series of prey evolution where only two morphs are possible. Under parameter values where Merilaita (2006, Fig. 2) found polymorphism to last for close to  $10^2$  generations, we find persistent polymorphism for the full  $5 \times 10^5$  time steps tested. For each of 100 runs, polymorphism persists throughout. We run the simulation for this high number of time steps to show the extent of the stability. Stochastic events can, by chance, lead to one morph becoming fixed in the prey population. At this point no amount of positive frequency-dependent predation can have any effect. With the inclusion of mutation however, the situation in which one morph becomes fixed in the population is a rare and tiny snapshot of the evolutionary dynamic, rather than an evolutionary end point. It is important to emphasize that



**Figure 1.** An example run, over  $5 \times 10^5$  time steps, showing the evolution of the prey species. Datapoints are plotted every 5000 time steps. Prey took the form of one of two morphs (with the prey population initially shared equally between each morph) and new offspring mutate between morphs with probability 0.0005. The solid line shows the proportion ( $p$ ) of prey of morph 1 (with the frequency of morph 2 being  $[1 - p]$ ). Parameters are set to  $P(j)_1 = 0.5$ ,  $P(j)_{\min} = 0.2$ ,  $P(j)_{\max} = 0.8$ ,  $m = 100$ , and  $n = 10$ . Polymorphism is persistent for the full  $5 \times 10^5$  time steps.

the polymorphism seen is not a trivial consequence of mutation alone. Mutation alone would only cause 0.05% of individuals on average to deviate from the majority morph. However, low levels of variation introduced by mutation can be amplified by apostatic selection to produce the high level of polymorphism seen in Figure 1, which shows a typical run.

#### THE EVOLUTION OF MULTIPLE MORPHS: EQUAL LEVELS OF DETECTABILITY

We first examine the model in which all morphs are equally detectable  $P(j)_1 = 0.5$ ,  $P(j)_{\min} = 0.2$ ,  $P(j)_{\max} = 0.8$ . Figure 2 shows the mean number of morphs evolved at the end of 100 replicates for variations of the parameters outlined in our methods. In the simulations without dietary wariness, the number of morphs increases with the strength of apostatic selection (although there is often considerable overlap in standard deviations between different turnover rates). The number of morphs generally increases when the intensity of predation is lower (i.e., when prey reproduce after 25%, rather than 50%, of the population has been killed; cf, Fig. 2A,B and Fig. 2C,D). Dietary wariness provides the most marked increase in the number of morphs evolved, almost to the maximum under some conditions (Fig. 2B,D). Predator life span has little effect without dietary wariness (although shorter life spans generally reduce the number of morphs; Fig. 2A,C). However, predator life spans and dietary wariness interact: shorter life spans increase the level of avoidance of novel morphs due to a higher turnover of naïve predators. The consequence is that di-

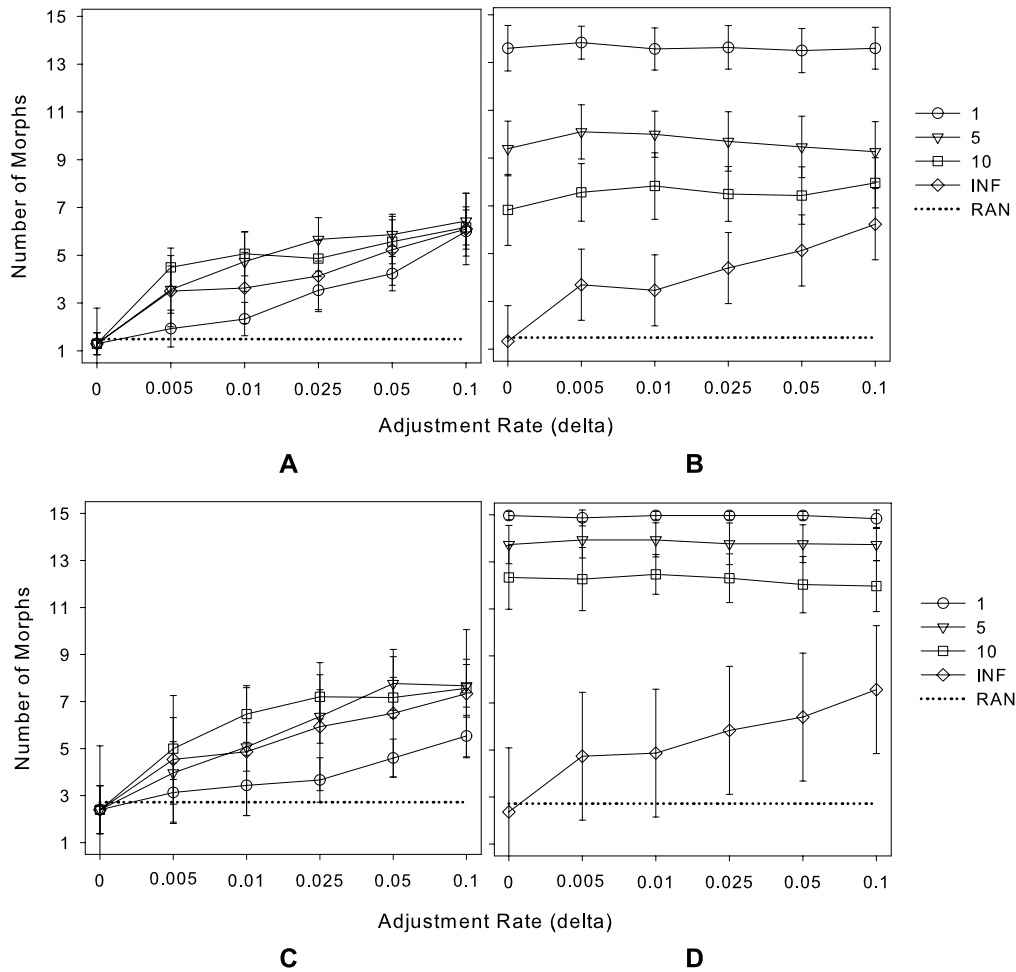
etary wariness and short predator life spans result in a very high number of morphs evolving (Fig. 2B,C). Without dietary wariness the number of morphs increases with the adjustment range, whereas predator life span has little significant effect. With dietary wariness a very high number of morphs are maintained, even when apostatic selection is absent, provided that predators are not too long-lived relative to prey. Under conditions of low predation rates, even with random predation (RAN), more than one morph is maintained in the population (Fig. 2C,D) because the equilibrium between new morphs being generated by “mutation” and lost through the stochastic element of predation (and reproduction) is raised.

When mutation creates a novel morph in the population, this morph comprises a very small number of individuals. The morph is therefore vulnerable because just a very few predation events can lead to its rapid extinction. Dietary wariness acts to reduce this risk, because a given predator is likely to encounter such prey extremely infrequently (because of their comparative rarity), often only once in its lifetime. Such an encounter will do the prey morph no harm. Thus, the rare morph will be afforded protection from predation while it is at low frequency, and will thus be less likely to become extinct and indeed will become more common in the population (through differential predation on other, more common, types). Because extinction risk will decline rapidly (faster than linearly) with increasing numbers of individuals, dietary wariness will contribute strongly to maintaining polymorphism.

#### THE EVOLUTION OF MULTIPLE MORPHS: ONE HIGHLY CRYPTIC AND MANY LESS-CRYPTIC MORPHS

In the cases of the Hawaiian happy-face spider, *T. gallator*, and the Californian *T. californicum*, there exists a single cryptic morph and many rare and seemingly more conspicuous morphs. We modify the model to reflect this situation, and start the prey species as monomorphic and cryptic. Detection probabilities and limits are set to  $P(1)_1 = 0.3$ ,  $P(1)_{\min} = 0.1$ ,  $P(1)_{\max} = 0.6$  for the single cryptic morph, and  $P(j)_1 = 0.7$ ,  $P(j)_{\min} = 0.5$ ,  $P(j)_{\max} = 1.0$  (where  $j = [2, \dots, 15]$ ) for all other morphs. Compared with the situation shown in Figure 2, where morphs are equally detectable, the presence of a cryptic morph generally lowers the total number of morphs that evolve (Fig. 3). However, high numbers of morphs still evolve where predators exhibit dietary wariness; particularly when predators have short life spans and where predation is low (Fig. 3B,D).

Figure 4 shows the frequencies of the cryptic and the pooled less-cryptic morphs at the end of each run, averaged over 100 replicates. Here, the predators exhibit dietary wariness and prey reproduce after half the population has been eaten (the simulation shown in Fig. 3B). In all cases, the cryptic morph always maintains a relatively high frequency, whereas the conspicuous morphs remain rare. The deviation at 0.005 for infinite (INF) (the



**Figure 2.** The mean number of morphs, over 100 replicates, evolved at  $t = 100,000$  (with standard deviations). The simulation was run with predators living for 1, 5, 10, and an infinite (INF) number of time steps (prey generations) before being replaced with new and naive predators, and with frequency-independent (and no dietary wariness) predation (RAN). In (A) and (C) predators do not exhibit dietary wariness, whereas in (B) and (D) they do. In (A) and (B) prey reproduce after 50% of the population has been killed. In (A) and (B) prey reproduce after 50% of the population has been killed, whereas in (C) and (D) they reproduce after 25% of the population has been killed. Parameters are set to  $P(j)_1 = 0.5$ ,  $P(j)_{\min} = 0.2$ ,  $P(j)_{\max} = 0.8$ ,  $m = 200$ , and  $n = 20$ .

case in which there is an infinite number of prey generations before predators are replaced by new, naive individuals) is simply stochastic, as evidenced by the large standard deviation.

Intuitively, if one morph achieves special protection from predation (at all frequencies) through being particularly cryptic, then this morph will generally dominate the prey population to the detriment of polymorphism. However, importantly we demonstrate that, providing this morph is not very highly undetectable, this effect will not be strong enough to prevent exuberant polymorphism evolving.

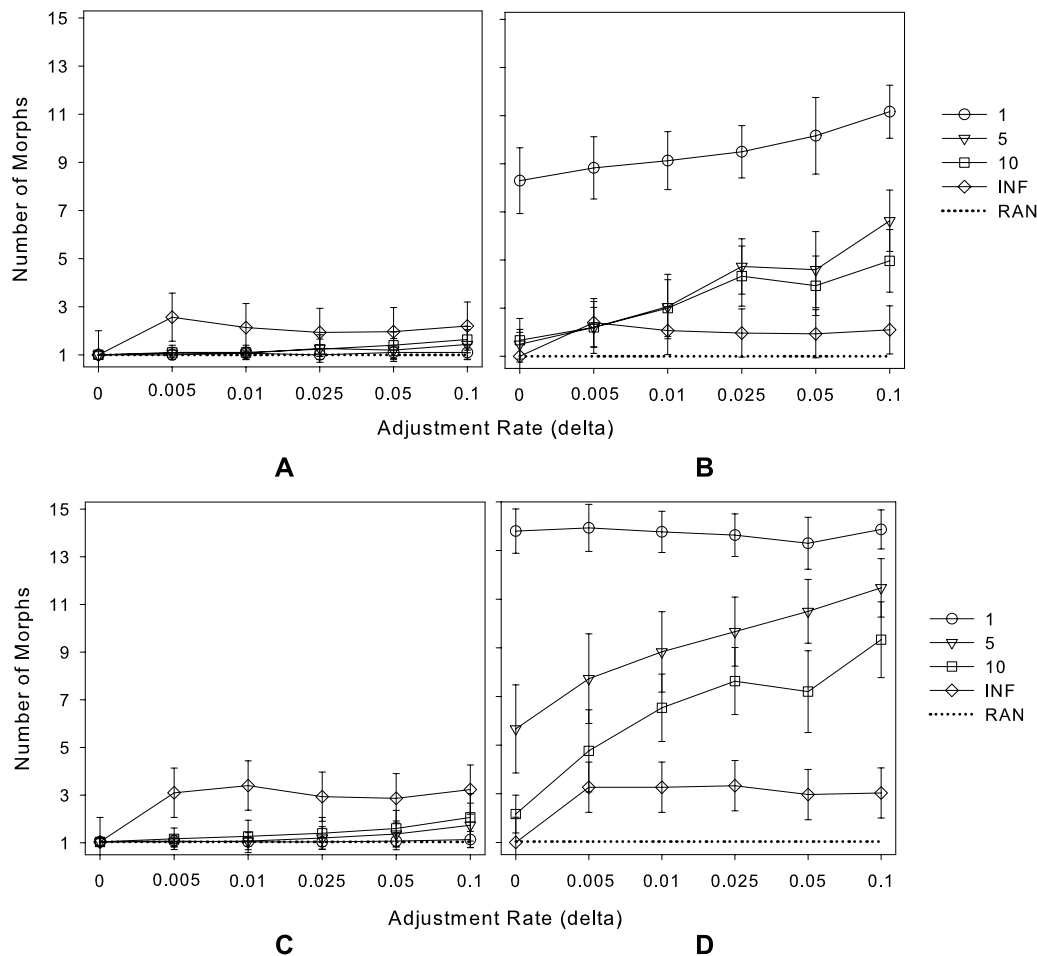
#### FURTHER ANALYSES

We model an alternative to the situation in which prey can evolve either cryptic or conspicuous forms, by allowing predators to build a search image for only cryptic prey (Reid and Shettleworth 1992), which we model as changing the probability of detectability only

after cryptic prey have been attacked. That is, the detection probabilities for each prey form are only updated when a predator attacks a cryptic individual. We find that this weakens the effects of apostatic selection further, making it an even less likely explanation for the evolution of many morphs (Fig. S1 cf Fig. 3). However, dietary wariness still has the effect of allowing multiple morphs to evolve. This is because dietary wariness is a form of frequency-dependent selection, and can act on morphs regardless of their level of conspicuousness.

We explore the effect of reducing the intensity of predation even further by assuming that prey reproduces after only 10% of the population has been killed. This results in a further upward shift in the number of morphs that evolve (Fig. S2; cf Fig. 3). We also examine the effect of varying the number of predators (Fig. S3) and the number of prey individuals (Fig. S4). We note that when the prey population size is low neither neophobia and/or





**Figure 3.** The mean number of morphs, over 100 replicates, evolved at  $t = 100,000$ . All parameters are the same as Figure 2, except one morph is more cryptic than the others. The simulation was run with predators living for 1, 5, 10, and an infinite (INF) number of time steps (prey generations) before being replaced with new and naïve predators, and with frequency-independent (and no dietary wariness) predation (RAN). In (A) and (C) predators do not exhibit dietary wariness, whereas in (B) and (D) they do. In (A) and (B) prey reproduce after 50% of the population has been killed, whereas in (C) and (D) prey reproduce after 25% of the population has been killed. Parameters are set to  $P(1)_1 = 0.3$ ,  $P(1)_{\min} = 0.1$ ,  $P(1)_{\max} = 0.6$  for the cryptic morph, and  $P(j)_1 = 0.7$ ,  $P(j)_{\min} = 0.5$ ,  $P(j)_{\max} = 1.0$  (where  $j = [2 \dots 15]$ ) for all other morphs.

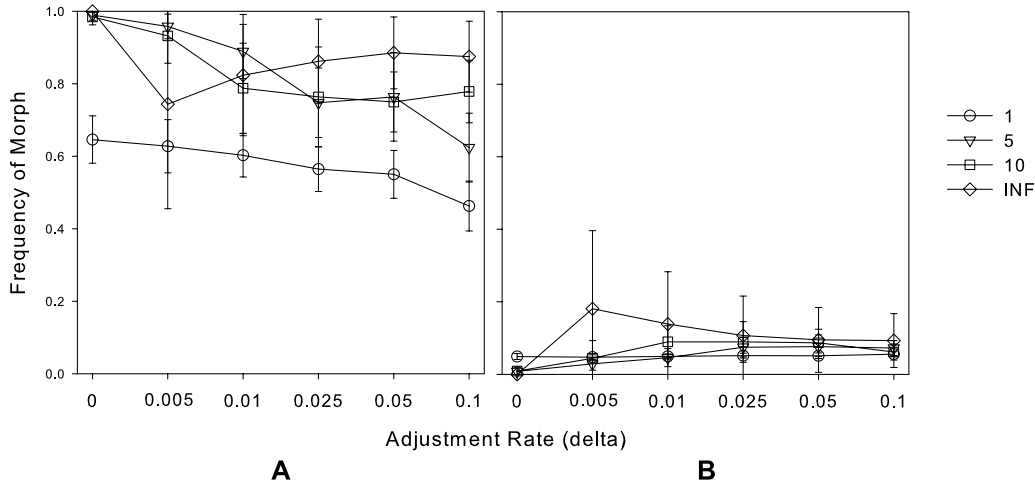
apostatic selection works particularly well. This is probably due to a reduced probability of mutation origination (i.e., there are fewer individuals to mutate) but mostly to less intense frequency-dependent effects when the population size is low. However, when the prey population size is higher we find that even more morphs evolve.

The temporal persistence of search images varies with situations and species (Bond 2007). So far, we have assumed that preferences resulting in apostatic selection are not forgotten, but merely modified as morph frequencies change. We additionally explore this situation by assuming that predators instantly and completely forget their search images after every 10 experiences with prey. Predators do not, however, forget which prey morphs they have introduced into their diet (i.e., they only exhibit dietary wariness once for each morph). Figure S5 shows the results of this

assumption. These results yet again confirm that apostatic selection alone cannot explain these types of polymorphisms, whereas dietary wariness can.

## Discussion

This study arose from attempts to understand the underlying mechanisms maintaining genetic polymorphisms in the spiders *T. grallator* and *T. californicum*. Although motivated by these species, our model applies to any general situation in which polymorphism arises, and explains the maintenance of high number of morphs, even when one morph is more cryptic than the others. Apostatic selection is often invoked as a mechanism for maintaining polymorphism, although it is usually stated that all prey morphs need to be cryptic in order for search image



**Figure 4.** The mean frequencies of morphs, over 100 replicates, evolved at  $t = 100,000$ . All parameters are the same as those in Figure 3b. Predators exhibit dietary wariness and prey reproduce after 50% of the population has been killed. (A) The mean frequency of the cryptic morph, and (B) the mean frequency of the other morphs (when active). The simulation was run with predators living for 1, 5, 10, and an infinite (INF) number of time steps before being replaced with new and naïve predators.

effects to manifest themselves (Bond 1983; Bond and Riley 1991; Langley 1996; Langley et al. 1996; Dukas 2002; Punzalan et al. 2005; Bond 2007). However, crypticity is relative. Data gathered by Popham (1941, 1942) on predation of the water bug *Arctocoris* (*Sigara distincta*) by fish were reanalyzed by Clarke (1962), who showed that even the most conspicuous form, when at low frequency, was predated less often than expected. Reid and Shettleworth's (1992) experiment 2 demonstrated that two of their four pigeons, pecking at two cryptic and one conspicuous grain "morphs," tended to over-predate the cryptic grain at high frequencies, and thus under-predated the conspicuous grain at low frequencies. At these frequencies, the other two birds took both cryptic and conspicuous prey in approximately the proportions presented. Finally, Bond and Kamil (1998), using birds to predate computer-generated prey, demonstrated the maintenance of less-cryptic forms at low frequencies. It may not follow therefore that in the present spider system, morphs that seem, to humans at least, not to be maximally cryptic are necessarily incapable of generating conditions under which apostatic selection is possible. However, our findings suggest that current understanding of the mechanisms of apostatic selection alone cannot explain the sheer number of morphs involved or the frequency distributions of morphs of varying crypticity (but see Bond and Kamil [1998]).

When all morphs are equally conspicuous and there is no dietary wariness, increasing the strength of apostatic selection and increasing ratios of predator to prey turnover rates lead to slightly higher number of morphs being maintained. However, the number of evolved morphs increases markedly when dietary wariness is introduced, with the greatest effect in situations in which the turnover rates of prey and predator are more similar. Indeed, with

predator populations turning over within the range one to 10 prey generations and dietary wariness, apostatic selection had virtually no influence on the number of morphs maintained. Lowering the proportion of prey eaten in each prey generation progressively increases the final number of evolved morphs (Figs. 2 and S2). These results suggest that a quite modest level of dietary wariness can, on its own, lead to the maintenance of large numbers of equally cryptic color morphs without the involvement of any other selective force, as is the case when the adjustment rate is set to zero (i.e., no apostatic selection). This is because dietary wariness is itself a form of negative frequency-dependent selection in that very rare morphs may be encountered only once during a prey generation and thus escape predation in our model. The cognitive processes responsible for neophobia (and dietary wariness generally) are different from those underlying selective attention and apostatic selection (Punzalan et al. 2005).

When we start our simulations with one cryptic morph and allow the evolution of less-cryptic forms, the effect is less dramatic than with equally detectable morphs. In the absence of dietary wariness, polymorphism only reliably evolves with a predator to prey turnover rate of one, and even then it involves only a few morphs. However, with dietary wariness and lower predation, appreciable numbers of morphs can be maintained. Our assumption that the number of possible cryptic morphs is limited while the number of less-cryptic morphs has fewer constraints can be justified by the fact that there are more ways to look different from a background than there are to match it (Sherratt and Franks 2005; Merilaita and Ruxton 2007; Franks et al. 2009). This point is likely to be particularly valid in the case of our example spider species, which spend the majority of their lives under leaves and thus against a relatively uniform green background.

We explore a range of relative turnover rates of predators compared to that of their prey. The spiders in question are essentially annuals and their predators, mostly small insectivorous birds, probably have average life spans of between two and four years. For example, among members of the Paridae in western, coastal North America, the range of *T. californicum* (Levi 1957), the average life span of the black-capped chickadee (*Poecile atricapillus*) is ca. 2.5 years (Smith 1991) and that of the oak titmouse (*Baeolophus inornatus*) is ca. 3.5 years (Cicero 2000). More generally, where predators live longer than their prey, biases toward consumption of particular color morphs might be lost if there is a period during the year when the specific prey species is either unavailable or at a stage too small to be worth foraging for. Within our model, therefore, the most likely relative turnover rate of prey to predators probably lie between the 1 and 5 bands, which happen to produce the highest number of morphs.

In parameterizing our model, we have tried, where possible, to use values that seem reasonable for the biological systems that stimulated our study. So, for example, in some simulations we model one cryptic morph and a number of (equally) less-cryptic forms, and the relative turnover rates of our predators is of the right order. We have had to assume an arbitrary figure for prey population sizes and the proportions of prey consumed in each predator generation—we just do not have relevant field data. It is also unclear to what extent the insectivorous birds assumed to be the likely predators of our spiders (members of the Fringillidae in Hawaii and the Paridae in North America) exhibit dietary wariness. In the wild, a transient neophobia alone may be effective in reducing predation on novel morphs if birds move rapidly through the vegetation gleaning prey. Given these considerations, we believe our parameterization of dietary wariness is probably conservative. Despite these uncertainties we have been able to simulate the evolution of a polymorphism with properties that match satisfyingly well the situation observed in the field for *T. grallator* and *T. californicum*. Our sensitivity analyses suggest that our results are both general and robust with respect to the relative effects of apostatic selection and dietary wariness on the evolution and maintenance of such exuberant polymorphisms.

We noted above the work of Thomas et al. (2004), who used an “evolving pastry bait” approach to study the fate of novel color morphs in palatable prey eaten by wild birds. Although not without their problems, similar experiments could offer a direct way of assessing the general results of the simulation models described here. In addition, it is essential to determine the distribution and properties of dietary wariness in predators of visibly polymorphic prey. This could indicate just how commonly the present models might apply in nature.

One of the inferences from our model is that the rare conspicuous morphs should be distinct from one another such that

neophobia or other aspects of dietary wariness are activated. In this respect, dietary wariness generates the same end point as apostatic selection, which is also predicted to lead to the evolution of distinctive morphs (Clarke 1962). It might also be expected that conspicuous morphs should be transient, with new highly divergent forms emerging repeatedly as the old ones eventually become too abundant, making them familiar to the birds and precipitating their rapid decline. In practice, however, the numbers of morphs might be limited by developmental constraints (Oxford 2009), and familiarity to the birds will be a complex function of the density of the polymorphic prey, the availability of alternative prey types, and the relative turnover rates of predators.

Dietary wariness (with or without apostatic selection) may also play a significant part in the evolution of massive polymorphisms. Here, many tens to hundreds of distinguishable morphs exist such that very large samples are required before two identical individuals are found (Moment 1962; Owen and Whiteley 1986, 1989; Weale and Allen 1989; Whiteley et al. 1997). It is difficult to envisage how traditional apostatic selection could operate to produce such a wealth of, individually very rare, morphs. Dietary wariness might hold the key, although the fact that rather few edible prey species are massively polymorphic suggests that a rather special combination of predators, prey, and background properties might be required (Bond and Kamil 2006).

The most important lesson to emerge from this study is that exuberant polymorphisms comprising tens of morphs can evolve solely on the basis of dietary wariness, irrespective of whether additional apostatic selection, through the development of search images (or other processes), is present or not. This effect of dietary wariness is enhanced when only a small proportion of the prey species is eaten before reproduction, perhaps as a result of abundant alternative food being available to the predator. Thus, other mechanisms, such as variation in search rates or apostatic selection via search images, are not necessary requirements for polymorphism. Conversely, apostatic selection alone is not a sufficient explanation for the maintenance of exuberant polymorphisms.

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## Supporting Information

The following supporting information is available for this article:

- Figure S1.** Results when search-images only apply to cryptic prey (c.f., Fig. 3 in text).
- Figure S2.** Results when prey reproduce after 10% of the population are killed.
- Figure S3.** Results when varying the number of predators.
- Figure S4.** Results when varying the number of prey.
- Figure S5.** Results when predators forget their search images.

Supporting Information may be found in the online version of this article.  
(This link will take you to the article abstract).

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