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## PERSPECTIVE:

### THE EVOLUTION OF WARNING COLORATION IS NOT PARADOXICAL

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*Abstract.*—Animals that are brightly colored have intrigued scientists since the time of Darwin, because it seems surprising that prey should have evolved to be clearly visible to predators. Often this self-advertisement is explained by the prey being unprofitable in some way, with the conspicuous warning coloration helping to protect the prey because it signals to potential predators that the prey is unprofitable. However, such signals only work in this way once predators have learned to associate the conspicuous color with the unprofitability of the prey. The evolution of warning coloration is still widely considered to be a paradox, because it has traditionally been assumed that the very first brightly colored individuals would be at an immediate selective disadvantage because of their greater conspicuousness to predators that are naive to the meaning of the signal. As a result, it has been difficult to understand how a novel conspicuous color morph could ever avoid extinction for long enough for predators to become educated about the signal. Thus, the traditional view that the evolution of warning coloration is difficult to explain rests entirely on assumptions about the foraging behavior of predators. However, we review recent evidence from a range of studies of predator foraging decisions, which refute these established assumptions. These studies show that: (1) Many predators are so conservative in their food preferences that even very conspicuous novel prey morphs are not necessarily at a selective disadvantage. (2) The survival and spread of novel color morphs can be simulated in field and aviary experiments using real predators (birds) foraging on successive generations of artificial prey populations. This work demonstrates that the foraging preferences of predators can regularly (though not always) result in the increase to fixation of a novel morph appearing in a population of familiar-colored prey. Such fixation events occur even if both novel and familiar prey are fully palatable and despite the novel food being much more conspicuous than the familiar prey. These studies therefore provide strong empirical evidence that conspicuous coloration can evolve readily, and repeatedly, as a result of the conservative foraging decisions of predators.

*Key words.*—Color choice, dietary conservatism, evolution of aposematism, foraging preferences, predation.

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Many animals, from a very wide range of taxonomic groups, have conspicuous coloration advertising their presence. This strategy seems a very risky one, since being noticed and attacked by predators is likely to reduce fitness. Some explanation is provided by the presence of chemical toxins or other defenses in most of these species, which deter predators once those predators have learned to associate the defense with the conspicuousness of the animal. After this association has been formed, there is an advantage to the prey to be conspicuous as this provides warning of its defense, reducing its likelihood of being attacked. This method of defense is termed “aposematism” (Poulton 1890), and is defined as the combination of unprofitability (e.g., physical

protection, chemical toxicity, or difficulty of capture) with one or more signals (such as warning or conspicuous coloration) warning of that unprofitability to potential predators. However, the evolution of aposematism still poses a problem since two traits (the signal and the unprofitability) must be present, and the signal understood by the predator, before this strategy is effective.

The evolution of warning coloration (the conspicuous signal given by the aposeme) is also a problem, because the first brightly colored individuals are widely assumed to be at a selective disadvantage and so appear likely to be driven to extinction before the predators learn the meaning of the signal. This traditional view therefore rests upon the assumption that the foraging decisions of predators place conspicuous novel prey morphs at a selective disadvantage. In this paper we discuss recent evidence that this assumption is not always correct.

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We begin with a review of current ideas about the possible evolutionary pathways by which aposematism could evolve, before discussing recent empirical evidence that conspicuous coloration can actually evolve readily, and repeatedly, as a result of the conservative foraging decisions of predators.

#### *Evolutionary Pathways to Aposematism*

Aposematism may evolve by any of three routes (Guilford 1988) from the presumed starting point of a cryptic population of profitable prey.

*Route 1: The prey become unprofitable, and then evolve a conspicuous signal to advertise this unprofitability.*—This evolutionary route is widely considered the most likely both by empiricists (Alatalo and Mappes 1996; Tullberg et al. 2000) and theoreticians (Harvey and Paxton 1981; Guilford 1988; Sillén-Tullberg 1988; Härlin and Härlin 2003) because many types of mutation can lead to the production of a defense. These include changes as relatively simple as the use of a new, toxic food plant or storage of toxic waste materials. Once such a defense arises, the trait will spread if it confers a net fitness advantage. If this new defense is effective enough to deter predators, it would be expected that any signal (such as bright coloration) that increases the detection rate, memorability, and ease of recognition will increase survival, because predators will kill fewer conspicuous defended prey by mistake. This assumes that the costs due to increased detectability to naive predators are more than counterbalanced by increased memorability to educated predators. This has been assumed only to be the case once the aposematic morph is sufficiently common for predators to learn avoidance through repeated encounters with unprofitable prey individuals of the same color pattern (Guilford 1988).

*Route 2: The conspicuous signal appears first, followed by the prey becoming unprofitable.*—This route is considered implausible in many cases (Harvey and Paxton 1981; Guilford 1988; Yachi and Higashi 1998; Riipi et al. 2001; Stuart-Fox et al. 2003) since conspicuous advertisements by undefended prey seem highly unlikely to be beneficial. Indeed, the loss of crypsis is widely considered likely to lead to the early demise of the first organism that gains this mutation. Even if the conspicuous signal is evolving for some other reason (e.g., sexual signaling), there will be considerable costs of conspicuousness, especially while the meaning of the signal is being established. However, as we describe below, recent studies call into question the assumption of high predation costs for undefended conspicuously colored novel prey morphs.

*Route 3: Unprofitability and conspicuous coloration arise simultaneously, or arise together in incremental steps.*—The chances of the two necessary mutations (for unprofitability and for the warning signal) occurring simultaneously are extremely small given normal mutation rates, so this possibility was initially discounted (Guilford 1988). However, recently (Lindström et al. 1999; Ruxton et al. 2004) it has been suggested that if a cryptic animal such as an insect becomes able to use a new food plant (e.g., through a mutation causing a change in digestive system or plant recognition system), it is likely to appear more conspicuous on this new plant than it was on the plant to which its cryptic coloration was orig-

inally adapted. If this new food plant contains a toxin that the insect prey is able to sequester and store without harm, but which is even mildly harmful to the insect's predators, then the increased conspicuousness can be used as a signal by those predators, allowing them to select the more profitable prey in preference to the less profitable (and more conspicuous) prey. In other words, the increase in conspicuousness, even at a very low level, acts as a signal of toxicity to the predator. If the level of conspicuousness can be used by predators as a cue (Sherratt 2002), subsequent selection will tend to increase the conspicuousness of that signal, and the toxicity of the defense until the prey are fully, classically, aposematic.

Each of these evolutionary paths to aposematism demands a solution to the same crucial problem. All require the initial survival and reproduction of a very rare conspicuous novel morph in a population of familiar cryptic prey (being defended in routes 1 and 3, and not in route 2). The initial survival of the novel morph must also be followed by an increase in its frequency until it is common enough for predators to learn about any association between the conspicuous color and the unprofitability of the morph. If the novel morph is not at first defended (route 2, above), then the morph must survive long enough for the acquisition of unprofitability and subsequent predator education.

The survival and increase in abundance of the new conspicuous morph is almost universally considered a serious obstacle because of the key assumption that the more conspicuous prey will get eaten first (Gittleman et al. 1980; Harvey and Paxton 1981; Mallet and Singer 1987; Endler 1988; Guilford 1990a,b; Schuler and Roper 1992; Alatalo and Mappes 1996; Yachi and Higashi 1998; Riipi et al. 2001; Stuart-Fox et al. 2003). If so, the first prey individuals to lose full crypsis, even if they are signaling honestly that they are unprofitable, would be likely to be killed before the predators can learn the meaning of the signal. If the prey are in fact toxic, predators may learn from this first experience, but (assuming the attack kills the prey) the original signaler is nonetheless extinct by then, so the trait cannot spread. Aggregation of closely related prey sharing the warning coloration may facilitate its subsequent spread (Riipi et al. 2001), but the problem of the survival of the first individual of any new conspicuous pattern remains. This conundrum depends on the well-worn assertion that predators will attack the most conspicuous prey given a choice between these and more cryptic prey.

In this paper, we review recent evidence for and against the assumption that novel prey morphs will be rapidly driven to extinction, and we present evidence that even very conspicuous novel prey can survive and spread in the face of predation pressure. We then discuss the implications of this finding for the evolution of aposematism.

#### *Evidence for Selection against Novel Forms*

The traditional view (reviewed in Guilford 1990b) that conspicuous forms will be attacked preferentially comes from two sources of reasoning: First, the existence of impressively accurate crypsis in a large number of species suggests a strong selective pressure against poorer crypsis in many contexts.

This leads to the assumption that conspicuousness (i.e., a large departure from crypsis) must be selected against. However, the observation that many undefended species lack accurate crypsis indicates that selection does not always favor the maximum degree of crypsis in undefended prey. Furthermore, it is at least possible that predators would react differently to a major color change in their prey than they would to a minor decrease in crypsis.

The second line of evidence supporting the classic view comes from experiments using domestic chicks (*Gallus gallus*) as predators. Chicks foraging on prey of two equally unfamiliar colors have been shown to consume the more conspicuous prey type in preference to a more cryptic prey type (Gittleman and Harvey 1980; Gittleman et al. 1980). However, these studies do not take into account the important effects of familiarity and novelty on predator behavior. In these experiments, both prey types were equally unfamiliar, whereas, as we describe below, a predator's foraging decisions may be profoundly influenced by its degree of familiarity with different color morphs of a particular prey type.

#### *Evidence for Selection Favoring Novel Forms*

Despite the studies described above, the assumption that conspicuous novel color morphs are usually at an initial selective disadvantage is questionable. For example, Coppinger (1969, 1970) found that avian predators often avoided novel insect prey. Similarly, Götmark (1992, 1993, 1994, 1996) demonstrated that conspicuous plumage in various songbird species reduced the chance that they would be attacked by birds of prey. Our own recent studies (Marples et al. 1998; Marples and Kelly 1999; Thomas et al. 2003, 2004) demonstrated that when a bird encounters a novel form of a given prey type in the presence of familiar versions of the same food type, it will generally prefer the familiar types and avoid the novel ones. This avoidance of novelty is independent of which color is novel and which color is familiar. This long-term avoidance of novel prey has been termed dietary conservatism (Marples et al. 1998) to distinguish it from neophobia (Barnett 1958), which is a much more short-lived aversion (lasting a few minutes at most) to approaching anything new. Dietary conservatism and neophobia appear to be based on fundamentally different learning processes (Marples and Kelly 1999). We often observe neophobia in our experimental animals (Marples et al. 1998; Marples and Kelly 1999; Kelly and Marples 2004), but even once neophobia has abated and the birds show no fear of approaching the novel food and occasionally pick it up, they do not necessarily consume it. Birds that pick up delicate prey species may cause them considerable damage (Mallet and Joron 1999), but this is much less than would be the case if their novelty did not evoke dietary conservatism, and the birds ate them. Dietary conservatism could facilitate the evolution of warning coloration, because if predators avoid novel prey for sufficient time, novel color morphs could invade a prey population and persist for some time, rather than suffering increased predation and rapid extinction (Coppinger 1969, 1970; Götmark 1994, 1996; Marples et al. 1998).

The duration of dietary conservatism is very variable between individuals of a given species, and can be extremely

long lasting in some individuals. For example, two free-living European blackbirds, *Turdus merula*, persisted for over two and a half years in their preference for one prey type, with which they had previously been familiarized, over a second prey type that was relatively novel (D. J. Kelly, unpubl. data). A large proportion of individuals show extended dietary conservatism (lasting weeks or months) in both of the wild species that we have studied (European robins *Erithacus rubecula* and European blackbirds; Kelly 2001). Some individuals are much less conservative and start eating new food quickly. This interindividual variation in the degree of dietary conservatism appears to have a genetic basis, at least in common quail *Coturnix coturnix* (Marples and Brakefield 1995) and great tits *Parus major* (Carere et al. 2001, 2003).

Some degree of dietary conservatism is present in every avian species explicitly tested thus far (common quail, Marples and Brakefield 1995; domestic chicks, Kelly 2001; European blackbirds, Marples et al. 1998; European robins, Marples and Kelly 1999; zebra finches *Taeniopygia guttata*, Kelly and Marples 2004), and the literature suggests its presence in a number of other species (snail kites *Rostrhamus sociabilis*, Beissinger et al. 1994; ring-billed gulls *Larus delawarensis* and herring gulls *Larus argentatus*, Rabinowitch 1968; scrub jays *Aphelocoma californica*, Sandoval 1994; Barbary doves *Streptopelia risoria*, Macleod 1978; song thrushes *Turdus philomelos*, Harvey et al. 1975; canaries *Serinus canaria*, Doherty and Cowie 1994; and red-winged blackbirds *Agelaius phoeniceus*, Neff and Meanly 1957). Dietary conservatism appears to be less extreme overall among birds held in captivity, but it is still clearly present. However, there are examples of dietary conservatism being so powerful in some captive individuals that they died of starvation rather than eat the novel food (domestic chicks, Rabinowitch 1965).

Birds are of course not the only group of predators that may have driven the evolution of novel color morphs (see below), but so far we know nothing about the degree of dietary conservatism of other predatory taxa. The few studies carried out on prey color choice in predatory dragonflies (Odonata; Kauppinen and Mappes 2003) and lizards (Sauria; Sandoval 1994; Krall et al. 1999; Cooper et al. 2000; Sword et al. 2000; Sword 2001) do not assess the role of novelty in responses to different prey color morphs.

#### *Empirical Simulations of the Evolution of Prey Color Morphs*

Knowing that a proportion of the population of any one predatory species is averse to eating novel forms of a known food does not necessarily mean that dietary conservatism can drive the evolution of aposematism. There arise a multitude of theoretical questions, for example, about how many predators would need to show high levels of dietary conservatism at any one site, so that less conservative individuals would not drive the novel morph to extinction, and how predators might behave as the novel morph becomes more familiar and more numerous. However, all such questions can be addressed together by offering a natural assemblage of predators a model system that mimics the starting conditions for the evolution of a new aposeme. The fate of the new conspicuous morph in the face of real predation can then be measured.

We used this approach to simulate evolution in the face of predation by real predators, using birds as a model class of predators, preying on successive generations of artificial prey populations. This tests directly how birds actually behave in such situations and led us to question the basic assumption that underlies the conundrum explored above; that predators will cause the rapid extinction of novel conspicuous prey morphs. If this assumption is inaccurate, then the evolution of aposematism may be relatively easy, because there may be no disadvantage to being the first conspicuously signaling prey individual and any, even slight, advantage may allow the conspicuousness trait to spread.

We have used this empirical simulation approach in a series of experiments designed to investigate the role of dietary conservatism in the evolution of aposematism, first using wild-caught European robins as the predators in an aviary study (Thomas et al. 2003) and subsequently using free-living bird assemblages coming to feeding stations in the wild (Thomas et al. 2004). In these studies we experimentally simulated the appearance of a single novel-colored mutant in small populations (20 individuals) of palatable artificial pastry "prey" of different colors, which were subjected to predation by birds. We familiarized the birds with one color of prey before introducing a second color as a novel "mutant" (treatments were balanced for color, to eliminate the effects of pre-existing color preferences). The novel morph always started as a single individual prey item and was represented in the population in subsequent "generations" (i.e., presented to the predators on each successive day of a trial) according to the proportions of each color morph surviving at the end of the previous day. Thus, the color morph frequencies in each successive "generation" of prey were determined by the relative survival of the previous generation under predation by experienced predators (whose experience presumably includes past encounters with real aposematic prey).

In many of the prey populations, these novel morphs became extinct within the first few generations (i.e., the proportion of novel prey in the population was driven to 0% in the first few days), but in other populations they survived and spread, eventually increasing to fixation (100%) in 35% of all prey populations when the experiment was carried out in an aviary (Thomas et al. 2003) and in 45% of the prey populations when the study was carried out in the wild (Thomas et al. 2004). We used Monte Carlo simulations to check that this result was not simply due to drift effects. These simulations were run using the results from the empirical experiments to define how many prey were "eaten" each day in the simulation (the same number as in the corresponding day in the empirical experiment), and the number of "days" for which the simulation was run. This simulation was used to calculate the likelihood of the novel morph increasing to fixation by chance. These simulations showed that the observed number of fixations were extremely unlikely to have occurred by chance, indicating active prey choice by the birds (for details of these simulations, see Thomas et al. 2003, 2004). Furthermore, the survival and increase to fixation of the novel conspicuous morph was recently demonstrated among larger populations (48 and 100 prey individuals per generation; R. J. Thomas, M. P. Speed, N. M. Mar-

ples, and D. J. Kelly, unpubl. data), in which fixation of novel morphs through drift effects is even less likely than in our original populations of 20 individuals.

These studies therefore demonstrated that the immediate demise of a fully palatable conspicuous new prey morph was not an inevitable outcome of predator behavior and that predation by birds regularly (though not always) resulted in the increase and spread of the novel morph, even reaching fixation in many populations. This occurred: (1) when both prey morphs were fully palatable; (2) when the novel food offered to wild birds was much more conspicuous than the familiar prey; (3) whether the novel color was associated with existing aposematic signals (red and yellow), or not (green and blue); (4) whether only one, or several, individual predators had access to each population; (5) when the novel prey were present over a number of generations (i.e., days) in increasing numbers (up to 18 days); and (6) when the novel prey were in the minority at first, and in the majority as it approached fixation, demonstrating that fixation can occur despite any effects of apostatic and/or antiapostatic selection for or against rarer prey types, respectively (Allen 1976).

In contrast to these empirical results, recently developed theoretical models that incorporated realistic levels of dietary conservatism (wariness) obtained from empirical data from wild European blackbirds (Marples et al. 1998; Kelly 2001), have predicted that the effects would be too short lived for the novel morph to spread (Ruxton et al. 2004). However, these models do not take into account the variation among individual predators in their level of dietary conservatism because they used only the average level of dietary conservatism for the whole predator population. However, it is increasingly accepted, that the variation among the individuals that make up the predator population must be taken into account for theoretical models to reflect the dynamics of natural systems (Speed 2001; Endler and Mappes 2004). Models incorporating the observed individual variation in dietary conservatism would be more realistic, as those individual predators that are more conservative than average are more likely to drive novel morphs to fixation in prey populations.

Our empirical simulation approach is powerful in that it directly investigates the effects of the actual foraging decisions of real predators, rather than relying on assumptions about the behavior of theoretical predators in a model. However, the extent to which our experiments can inform us about the evolution of the first aposematic individual of a new color pattern is limited by the similarity of our experiments to the natural situations in which such evolution may have taken place. For example, our prey were assumed to reproduce asexually, and their population sizes and generation times were smaller than is typical for most prey species (though not all; e.g., aphids [Aphidoidea]). The range of evolutionary outcomes across all possible parameters for predator and prey characteristics deserves further investigation using both empirical and theoretical simulations.

Nevertheless, our experiments show convincingly that the immediate demise of a fully palatable new prey morph is not an inevitable outcome of predator behavior, because the long-lived dietary conservatism of predators (rather than the more ephemeral effects of neophobia) often places novel prey at a selective advantage. We therefore argue that the costs pre-

viously believed to have been associated with the initial incidence of conspicuous morphs have been overstated, so that the evolution of aposematism need not be considered paradoxical. We must be cautious in extrapolating from these results in our study system, where all prey are palatable, to the case of new color morphs arising in prey where the familiar morph is already toxic, or otherwise defended (i.e., route 1, above). In this situation, the predator would have the choice of eating a prey it knows to be unprofitable (the familiar form) or consuming the novel form whose profitability is unknown. To decide what the predator would do we would need to know the relative strengths of its learned aversion to the familiar prey and its dietarily conservative aversion to the novel prey type. Tests in the laboratory (e.g., Mappes et al. 1999) suggest that the presence of an aversive prey may actually reduce predation on nearby novel prey, whatever their level of edibility. Similarly, in the wild, it is very possible that the predator may refuse both prey and eat something else instead. Further studies are needed to investigate the responses of predators to novelty in already defended systems.

*Is dietary conservatism a cause or a consequence of aposematism?*

We have so far been considering the survival and spread of a new palatable color morph in present-day ecosystems, where aposematism is a common feature of the environment. However, we must also consider how conspicuous warning coloration first evolved in predator-prey systems in which the predators had no previous experience of aposematic prey. In such a system, the predators would not have experienced selection for avoidance of aposematic colours per se, and so it could be argued that they therefore might not show dietary conservatism if this evolved as a response to the presence of aposematism in the environment. If this were the case, then the prey individuals that first evolved a conspicuous color pattern would be under a greater threat of predation from naive birds than they are now. Therefore, to consider the survival of conspicuous prey in the face of predation by naive predators, and their eventual evolution into aposematic animals, we need first to consider whether the dietary conservatism of predators is a cause or a consequence of the existence of aposematism. Specifically, did predators evolve their avoidance of novel prey in response to a world in which most unusual-looking prey were aposemes advertising their unprofitability, or did avoidance of novel prey by predators actually facilitate the evolution of the first aposematic signaling systems?

We believe that there are very good reasons to expect both neophobia and dietary conservatism even in a world without aposematic prey. Prey varies in its profitability, and sampling has costs in terms of time, energy and errors, even in the absence of toxicity. So, specialization on prey of known high quality can represent the optimal strategy under appropriate conditions (models reviewed in Stephens and Krebs 1986). Indeed, given the advantages of search images, experience with prey handling, and informational costs of a generalist foraging strategy (Dall and Cuthill 1997), it is likely that predators that are conservative in their diet would be at an

advantage even in an environment free of toxic prey. In addition, there is empirical evidence that fish (Bryan 1972; Roberts and Cheney 1974), amphibians (de Cock and Mathysen 2003), and reptiles (Sword et al. 2000; Sword 2001) can learn by taste aversion, and fish (Roberts and Cheney 1974; Figler and Einhorn 1983), garter snakes (Czaplicki et al. 1975), and even slugs (Delaney and Gelperin 1986) have been shown to exhibit neophobia, though no studies have addressed their dietary conservatism explicitly. Thus, we suggest that both neophobia and dietary conservatism are likely to be ancestral conditions in birds (and probably in many other predators too), predating aposematism.

*Evolution of Aposematism in Other Predator-Prey Systems*

It is clear that aposematism has evolved many times in different contexts and among a large number of diverse taxa. Among extant organisms, aposemes are dispersed widely but erratically across taxonomic groups, with fungi, plants, and both vertebrate and invertebrate animals all containing a number of diverse aposematic taxa as well as many nonaposematic taxa (Härlin and Härlin 2003). Furthermore, for example, phylogenetic evidence from dart poison frogs (Dendrobatidae; Summers and Clough 2001; Hagman and Forsman 2003; Santos et al. 2003) and coreoid bugs (Heteroptera; Zrzavy 1990) suggests multiple evolutionary origins even within these monophyletic groups. The repeated evolution of aposematism across and within a range of taxonomic groups constitutes strong evidence that aposematism can readily evolve in a wide range of ecological contexts and predator-prey systems.

The majority of empirical work on the evolution and spread of aposematism has considered birds as the predators and either insects or artificial food items as prey (Coppinger 1969; Guilford 1990a,b; Pinheiro 1996; Marples et al. 1998; Forsman and Merilaita 1999; Mappes et al. 1999; Gamberale-Stille and Tullberg 2001; Jetz et al. 2001; Riipi et al. 2001; Exnerová et al. 2003; Thomas et al. 2003, 2004) However, there are smaller collections of studies using lizards (Krall et al. 1999; Cooper et al. 2000; Sword et al. 2000; Sword 2001; Stuart-Fox et al. 2003) and fish (Bryan 1972; Roberts and Cheney 1974; Crossland 2001) as predators.

Most theoretical models use parameters drawn from the empirical literature on bird predators. A few have used human predators (Sherratt and Beatty 2003) but very few models have drawn on data from any other predatory groups despite the likelihood that higher vertebrates were absent at the time when the first aposemes arose (Kauppinen and Mappes 2003).

Despite this terrestrial bias in current studies, it is most likely that aposematism first arose in marine or aquatic ecosystems, and dietary conservatism might therefore be expected in these predators too. There is good evidence that marine invertebrates use aposematic signaling now (e.g., Ascidiarians [sea squirts]; Lindquist et al. 1992; Lindquist and Hay 1996, Nemertians [proboscis worms] and Opisthobranchs [sea slugs]; Tullrot 1994), and these groups date back to Cambrian times at least. The presence in marine environments of many other brightly colored toxic animals (e.g., sea slugs [Rudman 1991; Newman et al. 1994], flatworms [Newman et al. 1994; Ang and Newman 1998], anemones

[Schweitz et al. 1985; Mahnir and Kozlovskaya 1991; Malpezzi et al. 1993], and coral fish [Yasumoto and Murata 1993]), which are preyed upon by visually hunting predators (e.g., many predatory fish) supports the suggestion that aposomatic signaling is just as beneficial in the sea as it is on land and would have had far longer to evolve. We therefore need to extend our investigations of dietary conservatism into these ecosystems, rather than continuing to restrict our interest to terrestrial habitats.

Even in terrestrial ecosystems, the exclusive emphasis on avian predation gives an incomplete picture. Before birds evolved, the origin of warning coloration in terrestrial habitats is likely to have been driven by predatory insects; for example, dragonflies (Kauppinen and Mappes 2003) and mantids (Berenbaum and Miliczky 1984; Bowdish and Bultman 1993), amphibians such as frogs (Hatle et al. 2002) and toads (de Cock and Matthysen 2003), and reptiles (Sandoval 1994; Krall et al. 1999; Cooper et al. 2000; Sword et al. 2000; Sword 2001). So when birds evolved, there were almost certainly terrestrial aposomatic systems already in existence. Once birds evolved, they too would have exerted selective pressures on prey populations, which may have led to further evolutionary origins of aposematism.

Nevertheless, study of birds' responses to aposomatic prey is useful. It is highly likely that other predators, faced with the same sorts of problems of variable prey edibility with differing levels of conspicuousness, have evolved similar mechanisms for responding to such complexity. They will also have similar effects on the prey being eaten and produce similar evolutionary pressures. Thus, if we can work out how aposematism could spread in the bird-insect system we may learn which traits to look for in other (perhaps less experimentally convenient) marine or invertebrate predator-prey systems.

### Conclusion

We have argued that the evolution of aposematism is not a paradox, and that conspicuous novel prey morphs can, and do, readily survive and spread as the result of avian predator foraging decisions. The dietary conservatism exhibited by many avian predators serves to protect conspicuous novel morphs. Rather than such morphs being at a selective disadvantage, they may regularly enjoy a selective advantage, even though they are fully profitable prey, to the extent that they increase to fixation in many (though not all) prey populations. It is thereby possible for the evolution of aposematism to follow any of three routes: (1) signal-then-unprofitability, (2) unprofitability-then-signal, or (3) simultaneous evolution of signal and unprofitability. We emphasize that we are not arguing against one or another of these previously proposed pathways to aposematism, but we are simply demonstrating that they all appear to be possible, and that conspicuous aposomatic coloration can evolve readily, and repeatedly, as a result of the conservative foraging decisions of predators.

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