

Aposematic Coloration

Mathieu Joron

Leiden University

Insects attract collectors' attention because they are extremely diverse and often bear spectacular colors. To biologists, however, bright coloration has been a constantly renewed puzzle because it makes an insect a highly conspicuous prey to prospective predators. Charles Darwin understood that bright colors or exaggerated morphologies could evolve via sexual selection. However, he felt sexual selection could not account for the conspicuous color pattern of non-reproductive larvae in, for example, *Pseudosphinx* hawk moth caterpillars (Fig. 1). In a reply to Darwin about this puzzle, Alfred R. Wallace proposed that bright colors could advertise the unpalatability of the caterpillars to experienced predators. Indeed, prey that are not edible to predators are predicted to gain by exhibiting conspicuous and very recognizable colors; experienced predators can then correctly identify and subsequently avoid attacking such prey. E. B. Poulton later developed this idea, expanded it to other warning signals (i.e., sounds or smells), and coined the term "aposematism" to describe this phenomenon (from the Greek "away" and "sign").

Aposematic color patterns are found everywhere throughout the insects, from black- and yellow-striped stinging wasps to black and red, bitter-tasting lady beetles, or brightly colored, poisonous tropical butterflies. Although warning coloration has involved fascination, empirical and theoretical studies for some time, the puzzle of aposematism still motivates much debate today. First, although there is little doubt that bright coloration is often an antipredatory strategy, how aposematism evolves is far from clear. This is because brightly colored mutants in a population of cryptic (camouflaged) prey are more exposed to predators. How can a warning coloration evolve in a prey if the very first mutants exhibiting such coloration in the population are selected against? Second, the reasons for the brightness and conspicuousness of warning colors are not always clear and may be multiple. Are aposematic colors "road signs" that help predators learn better to differentiate inedible from edible prey, or are bright colors more easily memorized and associated to bad taste by predators? Did yellow and red colors, often borne by poisonous insects, evolve because of innate biases against these colors in the predators' brains, or are more complex cognitive, behavioral, frequency-dependent, or coevolutionary mechanisms involved in the evolution of warning patterns? Finally, why are warning patterns highly diverse in the insect world, whereas all toxic prey would gain by bearing the same color, thus reducing the probability of being sampled by a naïve predator?

WHAT TO ADVERTISE

"Aposematism is quite simply the correlation between conspicuous signals, such as bright coloration, and prey unprofitability," Candy Rowe wrote in 2001. But why should some prey become unprofitable in the first place, while others do not?



FIGURE 1 *Pseudosphinx tetrio* hawk moth caterpillar from the Peruvian Amazon showing a combination of red and black, classical colors used by aposematic insects. These larvae feed on toxic latex-sapped trees in the Apocynaceae. Length 14 cm. (Photograph © M. Joron, 1999.)

Unprofitability is difficult to define, and even more difficult to measure. It is certainly contextually defined, because the propensity of an animal to eat something is highly dependent on its level of hunger and its ability to use the prey for energy once eaten. Palatability (i.e., the predator's perception of prey profitability), greatly determines whether the predator will or will not eat the prey. Predator-prey coevolution led predators in part to rely on proximal perception to gauge the prey profitability. In particular, taste sensitivity may well have evolved in predators as an assessment of food toxicity: indeed, predators usually consider toxic chemicals to be distasteful. Some insects have external defenses such as horns, or spines, many of which cause irritation. Such physical defenses may be coupled to venom, as with the irritant hairs of many caterpillars or hymenopteran stingers. These insects may be otherwise perfectly profitable, and some predators evolve ways around the physical defenses, such as bee-eaters that are able to remove a bee's stinger and venom sac. Other insects have passive chemical defenses that predators discover upon consumption, such as chemicals in the hemolymph or sequestration glands of lubber grasshoppers or monarch butterflies. Such insects usually develop extra signals such as powerful smells, at least when handled, to advertise their toxicity before being consumed.

Toxicity is not the only way an insect can be unprofitable to predators. Difficulty in capturing prey (due to fast escape, erratic flight, breakable wings, etc.), or difficulty in handling prey (due to toughness or a hard cuticle) are other ways that insects can bring no net reward to the predators that spend energy chasing them, even if the chase results in the prey being seized. However, multiple unprofitability traits might be important in the evolution of warning signals.

Predators can have three kinds of response to a prey depending on their perception of prey profitability. If consuming a prey leads the predator to be more likely to attack similar prey in the future, perhaps even using the prey's appearance as a search image, the prey is called palatable. In feeding experiments, this usually leads birds to attack nearly 100% of the palatable prey offered. Of course, the predator may satiate after consuming a number of prey, and consequently the propensity to attack may decrease at high prey densities. In contrast, if experienced predators are less likely to attack similar prey, the prey is called unpalatable.

Of course, predators' memorizing capacity, and the strength of the prey unpalatability, may all influence how fast information regarding prey is acquired and how long it is retained.

However, a distasteful prey will inevitably lower the predator's instantaneous propensity to attack this prey further, an effect analogous to an immediate satiation. Finally, eating the prey may have no effect on the predator's subsequent behavior, which means that the prey is effectively neutral. This category is mainly derived from theory; there is little evidence that it exists in nature.

Variations in unpalatability among prey species, along what is called the "(un)palatability spectrum," affect the rate at which predators modify their behavior with experience. Predator's perceived toxicity is likely to be a sigmoid function of actual toxin concentration per unit prey mass, meaning that little of the palatability spectrum may fall into intermediate perceptions between "unpalatable" and "fully palatable." Although how predators learn is still under debate, experiments and theory suggest that they respond to a large extent to the (perceived) concentration of nasty chemicals they can tolerate per unit time.

The distastefulness of insects is generally linked to the host plants they utilize. Indeed, many distasteful or defended insects are herbivorous; most defended non-herbivorous insects are Hymenoptera. Some plant families, like the Solanaceae and the Passifloraceae, which are hosts to many chemically defended insects, contain alkaloids and cyanogens, respectively, as secondary metabolites. Some insects, like monarch butterflies (*Danaus plexippus*) that feed on *Asclepias* plants (milkweeds, Asclepiadaceae), sequester the compounds of such plants and store them; these insects thus avoid the toxic effects of the toxic compounds altogether. In soft-bodied insects (e.g., larvae), toxins are usually stored near the teguments or in special glands, ready to release their contents upon handling. The toxicity of insects that extract and sequester plant chemical compounds is dependent on the concentration of these compounds in the host plant. Sawfly larvae (Hymenoptera: Tenthredinidae), for example, reflex-bleed drops of hemolymph when touched; the unpalatability of such larvae is shown to be directly dependent on the glucosinolate concentration of their crucifer host plant over 24 h before "bleeding."

Other insects, however, synthesize their toxins *de novo*, like many chrysomelid beetles; they probably use the same enzymatic machinery that serves (or has served, in their ancestors) to detoxify the plant's secondary compounds. Although many of these species still use precursors derived from their food plant, these insects are usually less dependent on the plant's toxicity to develop their own noxious compounds. Some groups like ithomiine or heliconiine butterflies also get toxin precursors in their adult diet.

Whatever route to distastefulness is taken, we observe a general correlation between clades of distasteful insects and toxicity in host plant families. In butterflies, the distasteful Troidinae (Papilionidae) tend to feed on Aristolochiaceae, monarchs (Nymphalidae: Danainae) usually feed on milkweeds (Asclepiadaceae), longwing butterflies (Nymphalidae: Heliconiinae) feed on Passifloraceae, and clearwings (Nymphalidae: Ithomiinae) mainly on Solanaceae and Apocynaceae. In contrast, butterfly clades feeding on chemical-free monocotyledonous plants, like browns (Nymphalidae: Satyrinae) on grasses, or owl-butterflies (Nymphalidae: Brassoliniinae) on palms or Marantaceae, did not evolve distastefulness. Thus toxicity in insects may have evolved frequently as a by-product of adaptation to utilize

new kinds of food, particularly toxic plants. The costs of detoxification or toxin production could be covered by the benefits of invading competition-free hosts, perhaps assisted by the increased survival afforded by chemical protection.

DISGUSTING, BRIGHT, SIMPLE, AND CONTRASTED: WHY AND HOW TO ADVERTISE

Why should unprofitable prey advertise? Instead of parading with gaudy colors, why should all prey not try to escape predators' detection altogether through camouflage? Although the initial steps to aposematism are not obvious, the advantage of aposematic signals once established is clear. Indeed, numerous studies have shown that most predators are able to learn and recognize, and subsequently avoid, prey they associate with a bad experience.

Some distasteful prey, such as the transparent ithomiine butterflies found in the forest understory in tropical America, are not particularly conspicuous. The rampant mimicry found in this group of inconspicuous butterflies demonstrates that predators are able to learn and avoid such prey (although other stimuli, e.g., motion, might also be important). Still, most distasteful insects are brightly colored. Why should aposematic signals usually be conspicuous, and use simple color patterns of red, yellow, or black? Most of the answer is likely to be found in the cognitive behavior of the predators that selected for such colors. Several hypotheses have been put forward to explain the correlation between bright colors and unprofitability in insects. Bright contrasted colors are thought to be (1) easier to learn, (2) more difficult to forget, and (3) as different as possible from edible prey, thereby facilitating the avoidance of recognition errors. All these mechanisms are supported by experimental data to some extent (e.g., Fig. 2). Because both predators and aposematic prey benefit from correct identification, aposematic colors are believed to take advantage of any bias in the predator's cognition system. Likewise, predators in turn gain in being biased in the same direction as that taken by the prey. Therefore, prey signaling and predators' cognition are likely to have coevolved, which, incidentally, makes experimental evidence for any of the foregoing hypotheses generally hard to establish independently. Hypothesis 3 is the most likely to involve interactions between perception and cognition in the predators, leading to fast evolution of the prey's signals.

Many aposematic insects simultaneously send signals of different kinds, and some argue that such "multi modal" warning signals may reveal unconditioned biases that are absent when each sensory modalities is examined alone. Assuming that predators would rely solely on color and not behavior, motion, or sounds is perhaps simplistic, and it is sometimes argued that multiple signals could even be a prerequisite for the evolution of warning coloration

In fact, the reason for the apparent importance of multimodality probably lies again in the coevolutionary history of predators and their prey, which shapes innate biases. Predators are generally good entomologists for the potential prey they encounter often, and predators integrate various sensory modalities to make decisions regarding a particular action. Most aposematic insects are mimicked by edible species (Batesian mimics) that parasitize the warning function of the signal. The presence of these Batesian mimics reduces the reliability of the warning signal and means lost prey for the

predators. Model species may therefore escape being mimicked by evolving new dimensions for signaling, in addition to the established one (i.e., in different sensory dimensions).

Many warningly colored insects live in groups which enhances the warning function of their signal for three reasons (Fig. 3). First, predators tend to associate and retain noxiousness and a warning signal more quickly when presented with multiple copies of the same signal. Second, all unpalatable prey get an individual advantage in living in groups by the immediate avoidance, similar to the immediate satiation discussed earlier, caused in the individual predator that avoids the group altogether. Third, at the population level, clustering spatially also reduces the number of individual predators the population of prey is exposed to and has to educate, which again enhances the benefit of signaling. In short, it pays to be sitting right next to the toxic individual that is being sampled by a predator, because this is where the probability of predation is lowest, hence the advantage to living in groups. However, many solitary prey also exhibit warning coloration, and gregariousness does not necessarily evolve prior to aposematism.

One common mechanism leading to fast divergence in signals throughout the animals, known as peak shift, hinges here on the coupling of prey coloration, predator experience, and predator innate aversion. Prey can be placed on a conspicuousness axis (Fig. 4), with cryptic edible prey at one end (close to 0 conspicuousness) and incipient aposematic prey or new color pattern mutants at some distance down the axis. More conspicuous prey usually elicit stronger aversion in educated predators, which extrapolate the idea that stronger conspicuousness should mean stronger noxiousness. Therefore, stronger signals (away from edible prey appearance) lead to a supernormal response in the predators that thereby select for increased conspicuousness in the prey. This mechanism is a special case of runaway process and could be an important route to the evolution of aposematic prey that are bright and contrasted. It is thought that the coupling of such cognitive biases with the ability to learn leads to the selection of more strongly exaggerated warning colors and patterns in noxious prey than is expected in purely non-learning predators.

EVOLUTIONARY ROUTES TO APOSEMATIC COLORATION

The Problems

There are obvious benefits to bearing warning colors in a population of warning-colored prey. As noted by early naturalists like A. R. Wallace and E. B. Poulton, experienced predators avoid warningly colored prey, and presumably the number of prey killed during the predators' education is lower than in the absence of signaling. These benefits are clear at the group level but are not so clear at the individual level, because the first warningly colored individuals in a population of cryptic (and noxious) prey suffer strongly increased predation. Indeed, novel warningly colored prey not only suffer increased detection by prospective predators, but also elicit *no* avoidance in the predators. Consequently, there is strong positive frequency dependence, putting novel rare warning signals at a disproportionate disadvantage against an established strategy (crypsis, or another already established warning signal).

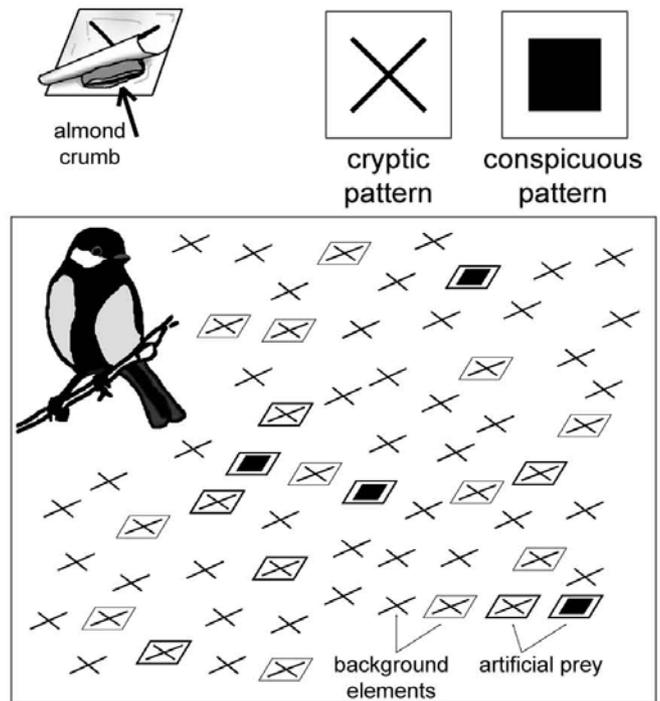


FIGURE 2 Schematic outline of the “novel world” experimental design developed by R. Alatalo and J. Mappes (University of Jyväskylä, Finland) to study the mechanisms of predator’s selection on conspicuous prey. Great tits, *Parus major*, are trained to forage in a room covered with small black symbols (e.g., crosses) on a white background, some of which are actual prey. Almond crumbs are placed between two 1-cm² pieces of paper glued together that bear a symbol on the outside. Black-squared prey items stand out conspicuously on the black-crossed background and represent potential warning signals, whereas black-crossed prey items are cryptic. The novelty of all symbols ensures that innate or previously learned prey recognition does not interfere with the predator’s response during the experiment. This setup also partly resolves one drawback of garden experiments, where the local food abundance for predators is artificially increased, making the searching costs, search images, and other predatory behavior unrealistic. By playing on the palatability of the prey items, it is possible to monitor how the birds learn to avoid the conspicuous signal. Mimics can also be incorporated in the environment at varying frequencies to study the dynamics of Batesian mimicry.

How could warning signals evolve at all if the first mutants using this strategy are killed? Laboratory experiments using the “novel world” design (Fig. 2) show rather unequivocally that aposematic patterns cannot evolve gradually in unpalatable prey. Indeed, small increases in visibility in cryptic prey increased attack rates without enhancing learning. Similarly, deviant phenotypes in established warning patterns suffered stronger predation. Finally, rare conspicuous prey suffered disproportionate predation, even when presented in groups. Therefore, a gradual increase in conspicuousness towards aposematism seems unlikely. This means that the evolving population must undergo a sudden jump, both in phenotype (to get a pattern that predators categorize as a different item) and in numbers beyond a threshold frequency (to allow the local predators to learn about the new pattern). Once the new pattern has achieved the minimum frequency and phenotypic thresholds, positive frequency dependence helps the new mutant to spread in the population. Peak shift or other processes can then occur, increasing the conspicuousness or adding other components to the signal. How can these evolutionary leaps be achieved — or circumvented — by an incipient aposematic prey?



FIGURE 3 Examples of gregarious warningly colored insects. (A) Gregarious *Chromacris* lubber grasshoppers nymphs (Orthoptera: Romaleidae) feeding on a toxic *Solanum mite*. Although it is not a bright color, black is often used as a warning color by insects, presumably because it increases conspicuousness by contrast against green foliage. (B) Gregarious *Morpho* sp. caterpillars spending the day in a dense cluster. They disperse at night for feeding. Clusters of aposematic prey often create an emergent, enhanced pattern presumably perceived as a supernormal stimulus by the predators and therefore better memorized. Caterpillars about 10 cm long. (Photographs from the Peruvian Amazon, © M. Joron, 1997.)

Deterministic Evolution via Immediate Benefits

NEOPHOBIA A new aposematic form could in theory escape the disadvantage of being rare and novel by causing immediate avoidance without having to be tasted at all by the predator. Indeed, predators are somewhat reluctant to sample novel-looking prey, particularly if novelty is associated with bright colors. This phenomenon is called “neophobia,” a kind of diet conservatism in predators. Neophobia could arise from various foraging biases, such as the formation of search images in the brains of predators as they search for edible-looking prey and ignore other prey, or via cultural inheritance, as with nestlings that tend to eat prey upon what they were fed by their parents. Neophobia is sometimes presented as a potential route toward aposematism. However, it does not really resolve the frequency dependence problem, because it is essentially a transient phenomenon involving no information acquisition by predators. Therefore as soon as numbers grow, however slightly, neophobia tends to vanish.

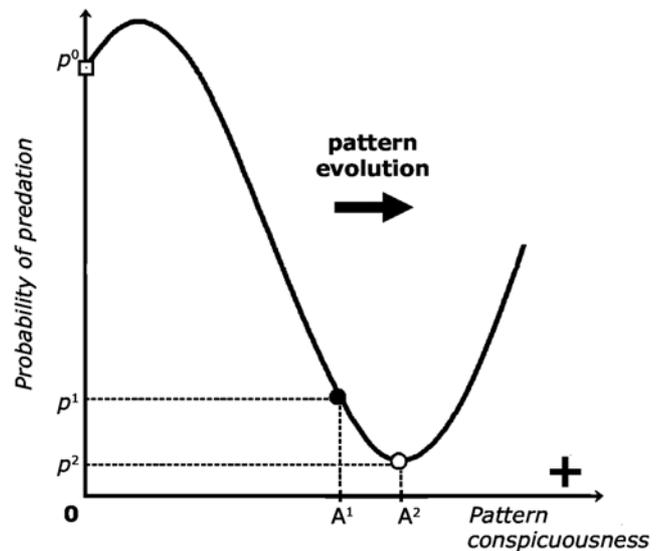


FIGURE 4 Peak shift mechanism applied to prey conspicuousness. The curve describes a fitness function that relates pattern conspicuousness to the probability of suffering predation. Predators are assumed to have knowledge of prey ranging from crypsis (open square: zero conspicuousness, palatability, high probability of predation) to aposematism (solid circle: high conspicuousness, A_1 ; unpalatability, low probability of predation, p_1). From this knowledge, predators extrapolate the palatability of prey with higher conspicuousness they have not yet experienced, hence the curve beyond the solid circle. In particular, slightly more conspicuous prey (open circle) elicit a stronger rejection response than the known aposematic prey (solid circle), and therefore suffer an even lower probability of predation, p_2 . Consequently, selection should cause the conspicuousness of the distasteful prey to shift gradually from A_1 to A_2 . In contrast, cryptic distasteful prey cannot drift away from crypsis (open square) toward higher levels of conspicuousness because they are more likely to be preyed upon when they become more conspicuous. An initial phenotypic jump is necessary to get to levels of conspicuousness where birds can categorize the prey as warningly colored, avoiding confusion with the normal staple of cryptic tasteful prey.

Neophobia should best be classified as a predator’s bias, like other innate biases against colors, smells, or sound, evolved by predators in response to their prey environment. Such biases are likely to channel the ultimate form taken by the aposematic signal (to the benefit of both preys and predators), but it is unlikely that they cause its evolution in the first place.

INDIVIDUAL ADVANTAGE One obvious way around initial obstacles is not to be killed by predators’ attacks. Then, prey could both educate the predators and be avoided in subsequent encounters. Indeed, most birds taste-test their prey before ingesting them, and many aposematic prey have noxious compounds in their outer parts, making it possible to be tasted but not injured by predators. For instance, ithomiine and danaine butterflies concentrate alkaloid in their wings. Day-flying pericopine moths let a voluminous and bitter hemolymph froth out of their body, likely tasted (or smelled) by a predator before it has profoundly injured the moth. Moreover, most unpalatable butterflies have very elastic bodies, which resist crushing. Strong smells that predators take as a warning for bad taste or toxicity, like those of stinkbugs, are another way by which prey can gain immediate advantage without having to be effectively tasted by the predators.

PREY ALREADY CONSPICUOUS Another way by which prey can overcome the difficulty of evolving conspicuous color is not to suffer any cost (i.e., avoid the necessity of a phenotypic leap) as a result of increased conspicuousness.

Indeed, most flying insects are rather conspicuous in flight and rely on their difficulty of capture to escape predation. They may not suffer any cost to bearing conspicuous colors, and indeed many butterflies, if not most, irrespective of their palatability, display bright patches of colors on the upper side of their wings, visible in flight, while having cryptic underwings making them inconspicuous when sitting. Such bright dorsal colors might initially evolve as sexual signals in male–male or male–female interactions long before unpalatability evolves. Once noxiousness has evolved, predators can learn an already conspicuous pattern without making recognition errors because of the resemblance to the palatable prey they have as search images. In a way, conspicuous flying insects can be said to be “preadapted” to evolve warning colors. But such patterns can then also change or drift according to predators’ biases. In particular, already bright color patterns can be enhanced toward brighter coloration through processes like peak shift, as described earlier. According to James Mallet, examples of this mechanism are the unpalatable *Taenaris* and *Hyantis* (Nymphalidae: Morphinae), which have evolved strikingly conspicuous warning spots via the enhancement of some of the less conspicuous eyespots that are still found on the undersides of their palatable relatives, the well-known blue *Morpho* butterflies.

MULLERIAN MIMICRY The easiest way to avoid the cost of rarity and conspicuousness altogether is to jump to an aposematic pattern already present in the habitat and known by the local predators. The shared appearance between several defended prey is called Müllerian mimicry, and it is likely that most aposematic species evolved via this route. Indeed, mimicry rings usually include a large number of Müllerian species (all of which are noxious). Of these, only one evolved the pattern first, followed by the other species that colonized an already protected pattern. This pattern of evolution is detectable by examining the biogeography and phylogeny of the species in question. For example, *Heliconius erato* and *H. melpomene* are Müllerian mimics throughout their distribution range. However, the *H. melpomene* was shown to have much younger color pattern races, with a clearly distinct genealogy, than *H. erato*, suggesting that *H. melpomene* is a Müllerian mimic that adopted the established color patterns of *H. erato*.

Population Processes: Kin Selection, Drift, and Shifting Balance

Because many unpalatable prey are indeed gregarious, it is easy to draw the conclusion that gregariousness allows the evolution of aposematism. The evolution of aposematism through gregariousness relies on the predator rejecting the whole group after sampling only one or few individuals. This extrapolation from one prey to the whole group is analogous to a superfast learning in the predator, which can be enhanced by conspicuousness. However, it also pays for aposematic preys to live in groups, thereby increasing their apparent density to the local predators. It is therefore not clear which of gregariousness or aposematism should evolve first to trigger the evolution of the other. Groups of gregarious larvae (Fig. 3) are usually family groups, suggesting that kinship might allow a new mutation quickly to get to a locally high frequency in such little-dispersing insects through kin selection. However, one should be aware that relatedness *per se* is not what favors the local rise in frequency of the gene here, but simply the local founding event by one or few family groups.

In fact, many adult aposematic adult insects are either not gregarious at all or do not aggregate in family groups. Besides, some of the most gregarious insect larvae come from the joint oviposition of several unrelated females. Although these examples could have arisen after the initial evolution of warning color through kin selection, it is more parsimonious to infer that non-kin-selection arguments can also explain the evolution of aposematism. Drift alone, particularly, followed by positive frequency dependence, is a good candidate mechanism (and in fact kin founding is only a special case of genetic drift). Indeed, when the ratio of predators to prey decreases in a locality, selection for antipredatory strategies is greatly diminished, allowing the exploration of other color pattern possibilities by the local population. Using release–recapture techniques of different warningly colored forms of *H. cydno* in Ecuador, D. Kapan showed that selection was relaxed when the butterflies were released in larger numbers. Therefore, the prey population could move via genetic drift above the required threshold, after which the new warning color invades the population.

Positive frequency-dependence has the interesting property that although it hinders the initial evolution of new patterns, it hinders the removal of any pattern once it has been established. If genetic drift in prey populations matches the fluctuations of selection pressures in time and space, new local aposematic patterns can be established frequently in different locations. These are essentially the first and second steps of the shifting balance theory of S. Wright. Competition between geographically adjacent warning color types then allows one pattern to spread to neighboring populations, like the traveling waves of color races documented in South America for *H. erato* or *H. melpomene*.

CONCLUSIONS

Despite the advantages of bearing a warning coloration established in the locality, the evolution of aposematism is not straightforward because proximal mechanisms seem to represent obstacles to its initial evolution. However, aposematic patterns are extremely diverse at all geographical and taxonomic levels, and this major discrepancy between theory and nature clearly suggests that positive frequency-dependent arguments are not as restrictive against the rise of novel warning colors. Similarly, predator generalization, which should not allow gradual shift of cryptic prey toward bright warning colors, does not seem to be efficient in restricting the rise of new conspicuous patterns. In fact, both population dynamics and psychological arguments might well explain such spectacular diversification. Firstly, positive frequency dependence would allow new local forms to be established through drift, relayed by other processes involving predator’s cognitive biases.

Secondly, the initial steps toward warning color are determined largely by which cognitive biases in the predators are exploited. That is, the initial pathway taken toward the evolution of warning coloration probably profoundly affects the aposematic phenotype the eventually evolves. Similarly, positive frequency dependence prevents deviations from the evolutionary pathway that is taken. In short, although aposematism is not expected predictably to evolve via Fisherian selection, it is such a powerful strategy once evolved that it is possibly inevitable in a contingent and varying world, where the nature and the height of the initial obstacles to its evolution fluctuate. It may thus follow a ratchet-like pattern of

evolution, where more routes may lead toward aposematism than routes away from it.

See Also the Following Articles

Chemical Defense - Crypsis - Mimicry - Monarchs

Further Reading

- Alatalo, R. V., and Mappes, J. (1996). Tracking the evolution of warning signals. *Nature*, **382**, 708–710.
- Edmunds, M. (1974). “Defence in Animals. A Survey of Anti-predator Defences.” Longman, New York.
- Endler, J. A. (1988). Frequency-dependent predation, crypsis, and aposematic coloration. *Philos. Trans. R. Soc. Lond. B* **319**, 505–524.
- Guilford, T. (1988). The evolution of conspicuous coloration. *Am. Nat.* **131**, S7–S21.
- Lindström, L., Alatalo, R. V., Lyytinen, A., and Mappes, J. (2001). Strong antiapostatic selection against novel rare aposematic prey. *Proc. Nat. Acad. Sci. U.S.A.* **98**, 9181–9184.
- Mallet, J., and Joron, M. (1999). Evolution of diversity in warning color and mimicry: Polymorphisms, shifting balance and speciation. *Annu. Rev. Ecolo. System* **30**, 201–233.
- Mallet, J., and Singer, M. C. (1987). Individual selection, kin selection, and the shifting balance in the evolution of warning colors: The evidence from butterflies. *Biolo. J. Linn. Soc.* **32**, 337–350.
- Poulton, E. B. (1890). “The Colours of Animals.” Trübner, London.
- Rowe, C. (ed.). (2001). Warning signals and mimicry. Special issue of *Evolutionary Ecology* [1999, vol. 13, no 7/8]. Kluwer, Dordrecht, The Netherlands.
- Sillén-Tullberg, B. (1988). Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. *Evolution* **42**, 293–305.
- Sword, G. A., Simpson, S. J., El Hadi, O. T. M., and Wilps, H. (2000). Density dependent aposematism in the desert locust. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 63–68.
- Wallace, A. R. (1879). The protective colours of animals. In “Science for All” (R. Brown, ed.), pp. 128–137. Cassell, Petter, Galpin., London.