= Aposematism =

Aposematism (from Greek ??? apo away , ? ? ??? sema sign , coined by Edward Bagnall Poulton) , perhaps most commonly known in the context of warning coloration , describes a family of antipredator adaptations in which a warning signal is associated with the unprofitability of a prey item to potential predators . Aposematism always involves an advertising signal . The warning signal may take the form of conspicuous animal coloration , sounds , odours or other perceivable characteristics . Aposematic signals are beneficial for both the predator and prey , since both avoid potential harm .

Aposematism is exploited in Müllerian mimicry , where species with strong defences evolve to resemble one another . By mimicking similarly coloured species , the warning signal to predators is shared , causing them to learn more quickly at less of a cost to each of the species .

Warning signals do not necessarily require that a species actually possesses chemical or physical defences to deter predators . Mimics such as the nonvenomous California mountain kingsnake (Lampropeltis zonata) , which has yellow , red , and black bands similar to those of the highly venomous eastern coral snake (Micrurus fulvius) , have essentially piggybacked on the successful aposematism of the model . The evolution of a warning signal by a mimicking species that resembles a species that possesses strong defences is known as Batesian mimicry .

= = Etymology = =

The term Aposematism was coined by the English zoologist Edward Bagnall Poulton in his 1890 book The Colours of Animals . He based the term on the Ancient Greek words ??? apo away , ?? ? ?? s?ma sign , referring to signs that warn other animals away .

= = Defence mechanism = =

The function of aposematism is to prevent attack , by warning potential predators that the prey animal has defences such as being unpalatable or poisonous . The easily detected warning is a primary defence mechanism , and the non @-@ visible defences are secondary . Aposematic signals are primarily visual , using bright colours and high @-@ contrast patterns such as stripes . Warning signals are honest indications of noxious prey , because conspicuousness evolves in tandem with noxiousness . Thus , the brighter and more conspicuous the organism , the more toxic it usually is . The most common and effective colours are red , yellow , black and white . These colours provide strong contrast with green foliage , resist changes in shadow and lighting , have strong contrast , are highly chromatic , and provide distance dependent camouflage . Some forms of warning colouration provide this distance dependent camouflage by having an effective pattern and colour combination that do not allow for easy detection by a predator from a distance , but are warning @-@ like from a close proximity , allowing for an advantageous balance between camouflage and aposematism . Warning colouration evolves in response to background , light conditions , and predator vision . Visible signals may be accompanied by odours , sounds or behaviour to provide a multi @-@ modal signal which is more effectively detected by predators .

Unpalatability , broadly understood , can be created in a variety of ways . Some insects such as the ladybird or tiger moth contain bitter @-@ tasting chemicals , while the skunk produces a noxious odour , and the poison glands of the poison dart frog , the sting of a velvet ant or neurotoxin in a black widow spider make them dangerous or painful to attack . Tiger moths advertise their unpalatability by either producing ultrasonic noises which warn bats to avoid them , or by warning postures which expose brightly coloured body parts (see Unkenreflex) , or exposing eyespots . Velvet ants (actually parasitic wasps) such as Dasymutilla occidentalis both have bright colours and produce audible noises when grabbed (via stridulation) , which serve to reinforce the warning . Among mammals , predators can be dissuaded when a smaller animal is aggressive and able to defend itself , as for example in honey badgers .

= = Prevalence = =

= = = In terrestrial ecosystems = = =

Aposematism is widespread in insects , but less so in vertebrates , being mostly confined to a smaller number of reptile , amphibian , and fish species . Perhaps the most numerous aposematic vertebrates are the poison dart frogs . Some plants are thought to employ aposematism to warn herbivores of unpalatable chemicals or physical defences such as prickled leaves or thorns . Many insects , such as cinnabar moth caterpillars , acquire toxic chemicals from their host plants . Among mammals , skunks and zorillas advertise their foul @-@ smelling chemical defences with sharply contrasting black @-@ and @-@ white patterns on their fur . Some brightly coloured birds such as passerines with contrasting patterns may also be aposematic , at least in females ; but since male birds are often brightly coloured through sexual selection , and their colouration is not correlated with edibility , it is unclear whether aposematism is significant .

= = = In marine ecosystems = = =

The existence of aposematism in marine ecosystems is controversial . Many marine organisms , particularly those on coral reefs , are brightly coloured or patterned , including sponges , corals , molluscs and fishes , with little or no connection to chemical or physical defenses . Caribbean reef sponges are brightly coloured , and many of them are chemically defended , but there is no relationship between the two factors .

Nudibranch molluscs are the most commonly cited examples of aposematism in marine ecosystems , but the evidence for this has been contested , mostly because (1) there are few examples of mimicry among species , (2) many species are nocturnal or cryptic , and (3) bright colours at the red end of the colour spectrum are rapidly attenuated as a function of water depth . For example , the Spanish Dancer nudibranch (genus Hexabranchus) , among the largest of tropical marine slugs , potently chemically defended , and brilliantly red and white , is nocturnal and has no known mimics . Mimicry is to be expected as Batesian mimics with weak defences can gain a measure of protection from their resemblance to aposematic species . Other studies have concluded that nudibranchs such as the slugs of the family Phyllidiidae from Indo @-@ Pacific coral reefs are aposematically coloured . Müllerian mimicry has been implicated in the colouration of some Mediterranean nudibranchs , all of which derive defensive chemicals from their sponge diet .

The crown @-@ of @-@ thorns starfish , like other starfish such as Metrodira subulata , has conspicuous coloration and conspicuous long , sharp spines , as well as chemical defences in the form of saponins ; this evidence is argued to be sufficient for such species to be considered aposematic . It has been proposed that aposematism and mimicry is less evident in marine invertebrates than terrestrial insects because predation is a more intense selective force for many insects , which also disperse as adults rather than as larvae and have much shorter generation times . Further , there is evidence that fish predators such as blueheads may adapt to visual cues more rapidly than do birds , making aposematism less effective .

Blue @-@ ringed octopuses are venomous . They spend much of their time hiding in crevices whilst displaying effective camouflage patterns with their dermal chromatophore cells . However , if they are provoked , they quickly change colour , becoming bright yellow with each of the 50 @-@ 60 rings flashing bright iridescent blue within a third of a second . It is often stated this is an aposematic warning display , although it is pointed out that such statements are often made without the hypothesis being tested .

= = Behaviour = =

The defence mechanism relies on the memory of the would @-@ be predator ; a bird that has once experienced a foul @-@ tasting grasshopper will endeavour to avoid a repetition of the experience .

As a consequence , aposematic species are often gregarious . Before the memory of a bad experience attenuates , the predator may have the experience reinforced through repetition . Aposematic organisms often move in a languid fashion , as they have little need for speed and agility . Instead , their morphology is frequently tough and resistant to injury , thereby allowing them to escape once the predator is warned off . Aposematic species do not need to hide or stay still as cryptic organisms do , so aposematic individuals benefit from more freedom in exposed areas and can spend more time foraging , allowing them to find more and better quality food . Aposematic individuals can similarly make use of conspicuous mating displays .

= = Origins of the theory = =

= = = Wallace , 1867 = = =

Alfred Russel Wallace suggested in a letter to Charles Darwin that the conspicuous colour schemes of some insects might have evolved through natural selection as a warning to predators . Darwin had proposed that conspicuous colouration could be explained in many species by means of sexual selection , but had realised that this could not explain the bright colouration of some caterpillars , since these larvae were not sexually active . Wallace replied that just as the contrasting coloured bands of a hornet warned of its defensive sting , so the bright colours of the caterpillar could warn of its unpalatability . Since Darwin was enthusiastic about the idea , in 1867 Wallace asked the Entomological Society of London to test the hypothesis . In response , the entomologist John Jenner Weir conducted experiments with caterpillars and birds in his aviary , and in 1869 he provided the first experimental evidence for warning colouration in animals .

= = = Poulton , 1890 = = =

The concept of warning colouration was extended by Edward Bagnall Poulton in The Colours of Animals (1890) :

When an animal possesses an unpleasant attribute , it is often to its advantage to advertise the fact as publicly as possible . In this way it escapes a great deal of experimental ' tasting . ' The conspicuous patterns and strongly contrasted colours which serve as the signal of danger or inedibility are known as Warning Colours ... It is these Warning Colours which are nearly always the objects of Protective Mimicry , and it will therefore be convenient to describe the former before the latter .

Poulton introduced the term aposematism in the same book with the words :

The second head (Sematic Colours) includes Warning Colours and Recognition Markings : the former warn an enemy off , and are therefore called Aposematic [Greek , apo , from , and sema , sign]

= = Evolution = =

Aposematism is paradoxical in evolutionary terms , as it makes individuals conspicuous to predators , so they may be killed and the trait eliminated before predators learn to avoid it . If warning colouration puts the first few individuals at such a strong disadvantage , it would never last in the species long enough to become beneficial .

= = = Supported explanations = = =

There is evidence for explanations involving dietary conservatism , in which predators avoid new prey because it is an unknown quantity ; this is a long @-@ lasting effect . Dietary conservatism has been demonstrated experimentally in some species of birds . Further , birds recall and avoid objects that are both conspicuous and foul @-@ tasting longer than objects that are equally foul @-@

tasting but cryptically coloured . This suggests that Wallace 's original view , that warning colouration helped to teach predators to avoid prey thus coloured , was correct . However , some birds (inexperienced starlings and domestic chicks) also innately avoid conspicuously coloured objects , as demonstrated using mealworms painted yellow and black to resemble wasps , with dull green controls . This implies that warning colouration works at least in part by stimulating the evolution of predators to encode the meaning of the warning signal , rather than by requiring each new generation to learn the signal 's meaning . All of these results contradict the idea that novel , brightly coloured individuals would be more likely to be eaten or attacked by predators .

= = = Alternative hypotheses = = =

Other explanations are possible . Predators might innately fear unfamiliar forms (neophobia) long enough for them to become established , but this is likely to be only temporary .

Alternatively , prey animals might be sufficiently gregarious to form clusters tight enough to enhance the warning signal . If the species was already unpalatable , predators might learn to avoid the cluster , protecting gregarious individuals with the new aposematic trait . Gregariousness would assist predators to learn to avoid unpalatable , gregarious prey . Aposematism could also be favoured in dense populations even if these are not gregarious .

Another possibility is that a gene for aposematism might be recessive and located on the X chromosome . If so , predators would learn to associate the colour with unpalatability from males with the trait , while heterozygous females carry the trait until it becomes common and predators understand the signal . Well @-@ fed predators might also ignore aposematic morphs , preferring other prey species .

A further explanation is that females might prefer brighter males , so sexual selection could result in aposematic males having higher reproductive success than non @-@ aposematic males if they can survive long enough to mate . Sexual selection is strong enough to allow seemingly maladaptive traits to persist despite other factors working against the trait .

Once aposematic individuals reach a certain threshold population , for whatever reason , the predator learning process would be spread out over a larger number of individuals and therefore is less likely to wipe out the trait for warning colouration completely . If the population of aposematic individuals all originated from the same few individuals , the predator learning process would result in a stronger warning signal for surviving kin , resulting in higher inclusive fitness for the dead or injured individuals through kin selection .

= = Mimicry = =

Aposematism is a sufficiently successful strategy to have had significant effects on the evolution of both aposematic and non @-@ aposematic species .

Non @-@ aposematic species have often evolved to mimic the conspicuous markings of their aposematic counterparts . For example , the hornet moth is a mimic of the yellowjacket wasp ; it resembles the wasp , but has no sting . A predator which avoids the wasp will to some degree also avoid the moth . This is known as Batesian mimicry , after Henry Walter Bates , a British naturalist who studied Amazonian butterflies in the second half of the 19th century . Batesian mimicry is frequency dependent : it is most effective when the ratio of mimic to model is low ; otherwise , predators learn to recognise the impostors .

A second form of mimicry occurs when two aposematic organisms share the same anti @-@ predator adaptation and mimic each other , to the benefit of both species , since fewer individuals of either species need to be attacked for predators to learn to avoid both of them . This form of mimicry is known as Müllerian mimicry , after Fritz Müller , a German naturalist who studied the phenomenon in the Amazon in the late 19th century . Many species of bee and wasp that occur together are Müllerian mimics ; their similar colouration teaches predators that a striped pattern is associated with being stung . Therefore , a predator which has had a negative experience with any such species will likely avoid any that resemble it in the future . Müllerian mimicry is found in vertebrates such as the

mimic poison frog (Ranitomeya imitator) which has several morphs throughout its natural geographical range , each of which looks very similar to a different species of poison frog which lives in that area .