Animal coloration

Animal coloration is the general appearance of an animal resulting from the reflection or emission of light from its surfaces . Some animals are brightly coloured , while others are hard to see . In some species , such as the peacock , the male has strong patterns , conspicuous colours and is iridescent , while the female is far less visible .

There are several separate reasons why animals have evolved colours . Camouflage enables an animal to remain hidden from view . Signalling enables an animal to communicate information such as warning of its ability to defend itself (aposematism) . Animals also use colour in advertising , signalling services such as cleaning to animals of other species ; to signal sexual status to other members of the same species ; and in mimicry , taking advantage of another species ' warning coloration . Some animals use colour to divert attacks by startle (deimatic behaviour) , surprising a predator e.g. with eyespots or other flashes of colour , and possibly by motion dazzle , confusing a predator 's attack by moving a bold pattern (such as zebra stripes) rapidly . Some animals are coloured for physical protection , such as having pigments in the skin to protect against sunburn , while some frogs can lighten or darken their skin for temperature regulation . Finally , animals can be coloured incidentally . For example , blood is red because the haem pigment needed to carry oxygen is red . Animals coloured in these ways can have striking natural patterns .

Animals produce colour in different ways . Pigments are particles of coloured material . Chromatophores are cells containing pigment , which can change their size to make their colour more or less visible . Some animals , including many butterflies and birds , have microscopic structures in scales , bristles or feathers which give them brilliant iridescent colours . Other animals including squid and some deep @-@ sea fish can produce light , sometimes of different colours . Animals often use two or more of these mechanisms together to produce the colours and effects they need .

History

Animal coloration has been a topic of interest and research in biology for centuries .

In his 1665 book Micrographia , Robert Hooke describes the " fantastical " (structural , not pigment) colours of the Peacock 's feathers :

The parts of the Feathers of this glorious Bird appear , through the Microscope , no less gaudy then do the whole Feathers ; for , as to the naked eye ' tis evident that the stem or quill of each Feather in the tail sends out multitudes of Lateral branches , ... so each of those threads in the Microscope appears a large long body , consisting of a multitude of bright reflecting parts .

... their upper sides seem to me to consist of a multitude of thin plated bodies , which are exceeding thin , and lie very close together , and thereby , like mother of Pearl shells , do not onely reflect a very brisk light , but tinge that light in a most curious manner ; and by means of various positions , in respect of the light , they reflect back now one colour , and then another , and those most vividly . Now , that these colours are onely fantastical ones , that is , such as arise immediately from the refractions of the light , I found by this , that water wetting these colour 'd parts , destroy 'd their colours , which seem 'd to proceed from the alteration of the reflection and refraction .

According to Charles Darwin 's 1859 theory of natural selection , features such as coloration evolved by providing individual animals with a reproductive advantage . For example , individuals with slightly better camouflage than others of the same species would , on average , leave more offspring . In his Origin of Species , Darwin wrote :

When we see leaf @-@ eating insects green , and bark @-@ feeders mottled @-@ grey ; the alpine ptarmigan white in winter , the red @-@ grouse the colour of heather , and the black @-@ grouse that of peaty earth , we must believe that these tints are of service to these birds and insects in preserving them from danger . Grouse , if not destroyed at some period of their lives , would increase in countless numbers ; they are known to suffer largely from birds of prey ; and hawks are guided by eyesight to their prey , so much so , that on parts of the Continent persons are warned not to keep white pigeons , as being the most liable to destruction . Hence I can see no reason to doubt that natural selection might be most effective in giving the proper colour to each kind of grouse , and in keeping that colour , when once acquired , true and constant .

Henry Walter Bates 's 1863 book The Naturalist on the River Amazons describes his extensive studies of the insects in the Amazon basin , and especially the butterflies . He discovered that apparently similar butterflies often belonged to different families , with a harmless species mimicking a poisonous or bitter @-@ tasting species to reduce its chance of being attacked by a predator , in the process now called after him , Batesian mimicry .

Edward Bagnall Poulton 's strongly Darwinian 1890 book The Colours of Animals , their meaning and use , especially considered in the case of insects argued the case for three aspects of animal coloration that are broadly accepted today but were controversial or wholly new at the time . It strongly supported Darwin 's theory of sexual selection , arguing that the obvious differences between male and female birds such as the Argus pheasant were selected by the females , pointing out that bright male plumage was found only in species " which court by day " . The book introduced the concept of frequency @-@ dependent selection , as when edible mimics are less frequent than the distasteful models whose colours and patterns they copy . In the book , Poulton also coined the term aposematism for warning coloration , which he identified in widely differing animal groups including mammals (such as the skunk) , bees and wasps , beetles , and butterflies .

Frank Evers Beddard 's 1892 book , Animal Coloration , acknowledged that natural selection existed but examined its application to camouflage , mimicry and sexual selection very critically . The book was in turn roundly criticised by Poulton .

Abbott Handerson Thayer 's 1909 book Concealing @-@ Coloration in the Animal Kingdom , completed by his son Gerald H. Thayer , argued correctly for the widespread use of crypsis among animals , and in particular described and explained countershading for the first time . However , the Thayers spoilt their case by arguing that camouflage was the sole purpose of animal coloration , which led them to claim that even the brilliant pink plumage of the flamingo or the roseate spoonbill was cryptic ? against the momentarily pink sky at dawn or dusk . As a result , the book was mocked by critics including Theodore Roosevelt as having " pushed [the " doctrine " of concealing coloration] to such a fantastic extreme and to include such wild absurdities as to call for the application of common sense thereto . "

Hugh Bamford Cott 's 500 @-@ page book Adaptive Coloration in Animals , published in wartime 1940 , systematically described the principles of camouflage and mimicry . The book contains hundreds of examples , over a hundred photographs and Cott 's own accurate and artistic drawings , and 27 pages of references . Cott focussed especially on " maximum disruptive contrast " , the kind of patterning used in military camouflage such as disruptive pattern material . Indeed , Cott describes such applications :

the effect of a disruptive pattern is to break up what is really a continuous surface into what appears to be a number of discontinuous surfaces ... which contradict the shape of the body on which they are superimposed .

= = Evolutionary reasons for animal coloration = =

= = = Camouflage = = =

One of the pioneers of research into animal coloration , Edward Bagnall Poulton classified the forms of protective coloration , in a way which is still helpful . He described : protective resemblance ; aggressive resemblance ; adventitious protection ; and variable protective resemblance . These are covered in turn below .

Protective resemblance is used by prey to avoid predation . It includes special protective resemblance , now called mimesis , where the whole animal looks like some other object , for example when a caterpillar resembles a twig or a bird dropping . In general protective resemblance , now called crypsis , the animal 's texture blends with the background , for example when a moth 's colour and pattern blend in with tree bark .

Aggressive resemblance is used by predators or parasites . In special aggressive resemblance , the animal looks like something else , luring the prey or host to approach , for example when a flower mantis resembles a particular kind of flower , such as an orchid . In general aggressive resemblance , the predator or parasite blends in with the background , for example when a leopard is hard to see in long grass .
For adventitious protection , an animal uses materials such as twigs , sand , or pieces of shell to conceal its outline , for example when a caddis fly larva builds a decorated case , or when a decorator crab decorates its back with seaweed , sponges and stones .
In variable protective resemblance , an animal such as a chameleon , flatfish , squid or octopus changes its skin pattern and colour using special chromatophore cells to resemble whatever background it is currently resting on (as well as for signalling) .
The main mechanisms to create the resemblances described by Poulton ? whether in nature or in military applications ? are crypsis , blending into the background so as to become hard to see (this covers both special and general resemblance) ; disruptive patterning , using colour and pattern to break up the animal 's outline , which relates mainly to general resemblance ; mimesis , resembling other objects of no special interest to the observer , which relates to special resemblance ; countershading , using graded colour to create the illusion of flatness , which relates mainly to general resemblance ; and counterillumination , producing light to match the background , notably in some species of squid .
Countershading was first described by the American artist Abbott Handerson Thayer , a pioneer in the theory of animal coloration . Thayer observed that whereas a painter takes a flat canvas and uses coloured paint to create the illusion of solidity by painting in shadows , animals such as deer are often darkest on their backs , becoming lighter towards the belly , creating (as zoologist Hugh Cott observed) the illusion of flatness , and against a matching background , of invisibility . Thayer 's observation " Animals are painted by Nature , darkest on those parts which tend to be most lighted by the sky 's light , and vice versa " is called Thayer 's Law .

= = = Signalling = = =

Colour is widely used for signalling in animals as diverse as birds and shrimps . Signalling encompasses at least three purposes :
advertising , to signal a capability or service to other animals , whether within a species or not
sexual selection , where members of one sex choose to mate with suitably coloured members of the other sex , thus driving the development of such colours
warning , to signal that an animal is harmful , for example can sting , is poisonous or is bitter @-@ tasting . Warning signals may be mimicked truthfully or untruthfully .

= = = = Advertising = = = =

Advertising coloration signals an animal 's capability to other animals . These may be of the same species , as in sexual selection , or of different species , as in cleaning symbiosis . Signals , which often combine colour and movement , may be understood by many different species ; for example , the cleaning stations of the banded coral shrimp Stenopus hispidus are visited by different species of fish , and even by reptiles such as hawksbill sea turtles .

= = = = Sexual selection = = = =

Darwin observed that the males of some species , such as birds of paradise , were very different from the females .
Darwin explained such male @-@ female differences in his theory of sexual selection in his book The Descent of Man . Once the females begin to select males according to any particular characteristic , such as a long tail or a coloured crest , that characteristic is emphasized more and more in the males . Eventually all the males will have the characteristics that the females are

sexually selecting for , as only those males can reproduce . This mechanism is powerful enough to create features that are strongly disadvantageous to the males in other ways . For example , some male birds of paradise have wing or tail streamers that are so long that they impede flight , while their brilliant colours may make the males more vulnerable to predators . In the extreme , sexual selection may drive species to extinction , as has been argued for the enormous horns of the male Irish elk , which may have made it difficult for mature males to move and feed .
Different forms of sexual selection are possible , including rivalry among males , and selection of females by males .

= = = = Warning = = = =

Warning coloration (aposematism) is effectively the " opposite " of camouflage , and a special case of advertising . Its function is to make the animal , for example a wasp or a coral snake , highly conspicuous to potential predators , so that it is noticed , remembered , and then avoided . As Peter Forbes observes , " Human warning signs employ the same colours - red , yellow , black , and white - that nature uses to advertise dangerous creatures . " Warning colours work by being associated by potential predators with something that makes the warning coloured animal unpleasant or dangerous . This can be achieved in several ways , by being any combination of :
distasteful , for example caterpillars , pupae and adults of the cinnabar moth , the monarch butterfly and the Variable Checkerspot butterfly have bitter @-@ tasting chemicals in their blood . One monarch contains more than enough digitalis @-@ like toxin to kill a cat , while a monarch extract makes starlings vomit .
foul @-@ smelling , for example the skunk can eject a liquid with a long @-@ lasting and powerful odour
aggressive and able to defend itself , for example honey badgers .
venomous , for example a wasp can deliver a painful sting , while snakes like the viper or coral snake can deliver a fatal bite .
Warning coloration can succeed either through inborn behaviour (instinct) on the part of potential predators , or through a learned avoidance . Either can lead to various forms of mimicry . Experiments show that avoidance is learned in birds , mammals , lizards , and amphibians , but that some birds such as great tits have inborn avoidance of certain colours and patterns such as black and yellow stripes .

= = = Mimicry = = =

Mimicry means that one species of animal resembles another species closely enough to deceive predators . To evolve , the mimicked species must have warning coloration , because appearing to be bitter @-@ tasting or dangerous gives natural selection something to work on . Once a species has a slight , chance , resemblance to a warning coloured species , natural selection can drive its colours and patterns towards more perfect mimicry . There are numerous possible mechanisms , of which by far the best known are :
Batesian mimicry , where an edible species resembles a distasteful or dangerous species . This is most common in insects such as butterflies . A familiar example is the resemblance of harmless hoverflies (which have no sting) to bees .
Müllerian mimicry , where two or more distasteful or dangerous animal species resemble each other . This is most common among insects such as wasps and bees (hymenoptera) .
Batesian mimicry was first described by pioneering naturalist Henry W. Bates . When an edible prey animal comes to resemble , even slightly , a distasteful animal , natural selection favours those individuals that even very slightly better resemble the distasteful species . This is because even a small degree of protection reduces predation and increases the chance that an individual mimic will survive and reproduce . For example , many species of hoverfly are coloured black and yellow like bees , and are in consequence avoided by birds (and people) .
Müllerian mimicry was first described by pioneering naturalist Fritz Müller . When a distasteful

animal comes to resemble a more common distasteful animal , natural selection favours individuals that even very slightly better resemble the target . For example , many species of stinging wasp and bee are similarly coloured black and yellow . Müller 's explanation of the mechanism for this was one of the first uses of mathematics in biology . He argued that a predator , such as a young bird , must attack at least one insect , say a wasp , to learn that the black and yellow colours mean a stinging insect . If bees were differently coloured , the young bird would have to attack one of them also . But when bees and wasps resemble each other , the young bird need only attack one from the whole group to learn to avoid all of them . So , fewer bees are attacked if they mimic wasps ; the same applies to wasps that mimic bees . The result is mutual resemblance for mutual protection .

= = = Distraction = = =

= = = = Startle = = = =

Some animals such as many moths , mantises and grasshoppers , have a repertory of threatening or startling behaviour , such as suddenly displaying conspicuous eyespots or patches of bright and contrasting colours , so as to scare off or momentarily distract a predator . This gives the prey animal an opportunity to escape . The behaviour is deimatic (startling) rather than aposematic as these insects are palatable to predators , so the warning colours are a bluff , not an honest signal .

= = = = Motion dazzle = = = =

Some prey animals such as zebra are marked with high @-@ contrast patterns which possibly help to confuse their predators , such as lions , during a chase . The bold stripes of a herd of running Zebra have been claimed make it difficult for predators to estimate the prey 's speed and direction accurately , or to identify individual animals , giving the prey an improved chance of escape . Since dazzle patterns (such as the Zebra 's stripes) make animals harder to catch when moving , but easier to detect when stationary , there is an evolutionary trade @-@ off between dazzle and camouflage . Another theory is that the zebra 's stripes could provide some protection from flies and biting insects .

= = = Physical protection = = =

Many animals have dark pigments such as melanin in their skin , eyes and fur to protect themselves against sunburn (damage to living tissues caused by ultraviolet light) .

= = = Temperature regulation = = =

Some frogs such as Bokermannohyla alvarengai , which basks in sunlight , lighten their skin colour when hot (and darkens when cold) , making their skin reflect more heat and so avoid overheating .

= = = Incidental coloration = = =

Some animals are coloured purely incidentally because their blood contains pigments . For example , amphibians like the olm that live in caves may be largely colourless as colour has no function in that environment , but they show some red because of the haem pigment in their red blood cells , needed to carry oxygen . They also have a little orange coloured riboflavin in their skin . Human albinos and people with fair skin have a similar colour for the same reason .

= = Mechanisms of colour production in animals = =

Animal coloration may be the result of any combination of pigments , chromatophores , structural coloration and bioluminescence .

= = = Coloration by pigments = = =

Pigments are coloured chemicals (such as melanin) in animal tissues . For example , the Arctic fox has a white coat in winter (containing little pigment) , and a brown coat in summer (containing more pigment) . Many animals , including mammals , birds , and amphibians , are unable to synthesize most of the pigments that colour their fur or feathers , other than the brown or black melanins that give many mammals their earth tones . For example , the bright yellow of an American goldfinch , the startling orange of a juvenile red @-@ spotted newt , the deep red of a cardinal and the pink of a flamingo are all produced by carotenoid pigments synthesized by plants . In the case of the flamingo , the bird eats pink shrimps , which are themselves unable to synthesize carotenoids . The shrimps derive their body colour from microscopic red algae , which like most plants are able to create their own pigments , including both carotenoids and (green) chlorophyll . Animals that eat green plants do not become green , however , as chlorophyll does not survive digestion .

= = = Variable coloration by chromatophores = = =

Chromatophores are special pigment @-@ containing cells that can change their size , thus varying the colour and pattern of the animal . The voluntary control of chromatophores is known as metachrosis . For example , cuttlefish and chameleons can rapidly change their appearance , both for camouflage and for signalling , as Aristotle first noted over 2000 years ago :

The octopus ... seeks its prey by so changing its colour as to render it like the colour of the stones adjacent to it ; it does so also when alarmed .

When cephalopod molluscs like squid and cuttlefish find themselves against a light background , they contract many of their chromatophores , concentrating the pigment into a smaller area , resulting in a pattern of tiny , dense , but widely spaced dots , appearing light . When they enter a darker environment , they allow their chromatophores to expand , creating a pattern of larger dark spots , and making their bodies appear dark . Amphibians such as frogs have three kinds of star @-@ shaped chromatophore cells in separate layers of their skin . The top layer contains ' xanthophores ' with orange , red , or yellow pigments ; the middle layer contains ' iridophores ' with a silvery light @-@ reflecting pigment ; while the bottom layer contains ' melanophores ' with dark melanin .

= = = Structural coloration = = =

While many animals are unable to synthesize carotenoid pigments to create red and yellow surfaces , the green and blue colours of bird feathers and insect carapaces are usually not produced by pigments at all , but by structural coloration . Structural coloration means the production of colour by microscopically @-@ structured surfaces fine enough to interfere with visible light , sometimes in combination with pigments : for example , peacock tail feathers are pigmented brown , but their structure makes them appear blue , turquoise and green . Structural coloration can produce the most brilliant colours , often iridescent . For example , the blue / green gloss on the plumage of birds such as ducks , and the purple / blue / green / red colours of many beetles and butterflies are created by structural coloration . Animals use several methods to produce structural colour , as described in the table .

= = = Bioluminescence = = =

Bioluminescence is the production of light , such as by the photophores of marine animals , and the tails of glow @-@ worms and fireflies . Bioluminescence , like other forms of metabolism , releases energy derived from the chemical energy of food . A pigment , luciferin is catalysed by the enzyme luciferase to react with oxygen , releasing light . Comb jellies such as Euplokamis are bioluminescent , creating blue and green light , especially when stressed ; when disturbed , they secrete an ink which luminesces in the same colours . Since comb jellies are not very sensitive to light , their bioluminescence is unlikely to be used to signal to other members of the same species (e.g. to attract mates or repel rivals) ; more likely , the light helps to distract predators or parasites . Some species of squid have light @-@ producing organs (photophores) scattered all over their undersides that create a sparkling glow . This provides counter @-@ illumination camouflage , preventing the animal from appearing as a dark shape when seen from below . Some angler fish of the deep sea , where it is too dark to hunt by sight , contain symbiotic bacteria in the ' bait ' on their ' fishing rods ' . These emit light to attract prey .