REVIEW ARTICLE

SOME ASPECTS OF CAMOUFLAGE IN ANIMALS

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ABSTRACT

Camouflage is the principal device by which vulnerable animals escape predation. The attention of potential predators can be avoided by protective resemblance mimicking an inedible object such as a seed or leaf. Concealment is achieved by means of colours that match the general environment, obliterative countershading, transparency, disruptive and coincident coloration, and by projections that break up the outline of the body. Vertebrate eyes tend to be very conspicuous unless their shape is disrupted by black eye-stripes. Adventitious materials may be used both for disguise and to make the animals that carry them distasteful to predators. Deflection of attack is sometimes achieved by autotomy or by deflection marks.

Many of these principles are invoked in the protection of the young. Finally, camouflage and disguise may be used for offence as well as for defence. Numerous examples of camouflage are cited, but the vast topic of mimicry has not been discussed.

INTRODUCTION

Some years ago, my wife and I spent a week at Watamu, between Malindi and Mombasa, on the coast of Kenya. From amongst the leaf litter beneath the trees a few metres inland from the beach, I collected a number of giant black millipedes. With their hardened integumental armour and batteries of poison glands that can squirt a concentrated solution of cyanide at an aggressor, it is not surprising that animals should have few predatory enemies. Indeed, their conspicuous black aposematic colour probably ensures that they are not inadvertently molested. I placed them in a glass jar, along with some vegetable debris and leaf litter to keep

them damp, and showed them to my wife. But what interested her more than the millipedes was something that until then, I had assumed to be a winged seed but which, under her scrutiny, had moved an antenna, there by disclosing its true identity a tenebrionid beetle of the genus *Cossyphus* (Fig. 1). The wing cases of the insect were greatly extended so that it had a flattened, oval shape, while its body was only slightly thickened on the ventral side. Until the beetle moved one of its antennae it could not be recognised for what it was (Cloudsley-Thompson 1978, 1980).

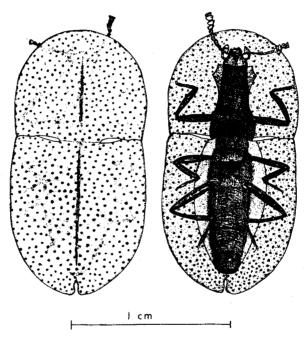


Fig. 1: Camera lucida drawing of *Cossyphus sp.* from East Africa, showing resemblance to a winged seed. Left: dorsal; right: Ventral view.

This stunning example of 'protective resemblance' was by no means the only instance of camouflage that we met with at Watamu. The beach was inhabited by ghost-crabs (Ocypode ceratophthalma) which scuttled silently away whenever we approached them. Although we could see them perfectly clearly while they were on the move, they became invisible the moment they stopped running. Not only did their pale colour match exactly the coral sands on which they lived, general colour resemblance to the background, but they sheltered instinctively in natural hollows where their shadows were concealed. It is the absence of shadow which gives the small crabs their ghostly appearance (Cott 1929, 1940).

PRINCIPLES OF CAMOUFLAGE

Cast up by the waves were the shells of a number of pelagic winkles (*lanthina ianthina*). These tropical marine molluscs, common in Indo-Pacific waters, hang upside down, floating beneath bubbles of hardened slime. Their bodies and the ventral parts of their shells are deep purple, like the colour of the sea, but the upper whorls are pale (Edmunds 1974). Unless they crouch flat on the ground like ghost-crabs, animals which are not transparent can only conceal their natural shadows by 'obliterative counter-shading' (Cott 1940). A counter-shaded animal's back is usually of a deeper hue than its flanks so that shadows are not apparent. Animals such as the purple sea-snail which normally rest upside down, show reversed counter-shading with the dorsal surface pale and the ventral, which is now the upper, surface pigmented.

But it is not necessary to go to the tropics to find examples of reversed counter-shading. When resting among the leaves of sallow, their food plant, caterpillars of the hawk-moth (Smerinthus ocellatus) do so in an inverted posture, suspended with only the hinder pairs of claspers clinging to the stem. In this position the underparts are fully illuminated from above, while the back is in shade. Because they are counter-shaded, however, all appearance of solidity is destroyed and the larvae are so difficult to see that it is often easier to find the leaves which they have been nibbling and then feel for them nearby (Cott 1940). Some midwater squids respond to overhead illumination by turning on numerous downwardly directed photophores which make them invisible when the intensity of the photophores matches that of the illumination. These results strongly support the theory of ventral bioluminescent counter-shading (Young and Roper 1976).

Silvery fishes are better camouflaged than normally counter-shaded fish because they reflect the light when viewed from the side. More difficult to detect in water, however, are jelly-fishes and Ctenophora, because they are transparent. Consequently, they have no shadow, they cannot be seen against any background, and movement does not give them away as it does the ghost-crabs on the shore (Chapman 1976). There were many jelly-fishes in the sea at Watamu including the Portuguese man-of-war *Physalia pelagica*). These were all small-not exceeding 4 cm in length. Even so, when I got stung while bathing in rough water, there were painful local reactions, a swelling of nearby glands and unpleasant generalized symptoms which persisted for more than an hour. Large specimens, with floats 30 cm long and tentacles up to several metres in length, have been reputed, on occasion, to cause the death of human victims. With such powerful defences, one might wonder why Portuguese men-of-war should need to be transparent. Possibly

they are preyed on by enemies immune to their stings: at the same time, the crustaceans and fishes on which they themselves feed are unable to see and avoid them. They are cryptic both in defence and in offence.

DISRUPTIVE COLORATION

The success of a conjuror often depends upon his ability to distract attention away from the act of deception by creating a secondary diversion of some kind. A similar principle is employed by animals that escape detection by means of disruptive coloration or dazzle patterns that catch the eye of the observer but draw his attention away from the shape of the creature that bears them. The patterns themselves may be conspicuous enough, but they camouflage the characteristic outline of the animal they adorn. The black stripes that cross the bodies of many tropical fishes and amphibians for instance - especially those that cross the eyes serve to render the animals almost indistinguishable in their normal environment.

Disruptive coloration consists of a superimposed pattern of colours and tones which break up the outline of an animal's body. Examples are to be found throughout the animal kingdom. They can be seen, for instance, in the pale, dorsal stripes of different grasshoppers, mantids and caterpillars, in the irregular blotches of dark colour that characterize the skins of amphibians and reptiles, in the stripes of weed-dwelling fishes, and in the camouflaged fur of forest mammals. Disruptive coloration, or dazzle patterns, as they are sometimes inappropriately called, contradict the form of the animal on which they are superimposed. A dramatic example, is afforded by the European ringed plover (Charadrius hiaticula), a bird whose eggs and young are mottled and extremely cryptic - as is the adult, when at rest, because its shape is distorted by the white collar, wing-bars and white-tipped tail. Other fine examples of camou-flaged eggs are provided by the buff and black eggs of the lapwing (Vanellus vanellus) and those of the stone curlew (Burhinus oedicnemus), among the most difficult of all to find. These are in striking contrast to the white, unpigmented eggs of birds whose nests are hidden in holes (Cott 1940, Edmunds 1974).

Sometimes the disruptive principle is extended not only to break up the continuous surface of the body, but to make the separate parts of the body appear to be joined together. This phenomenon is known as 'coincident disruptive coloration', and a familiar example is afforded by the common frog (Rana temporaria), whose hind limbs exhibit transverse bands of light and dark colours. When these legs are folded up at rest, one or more of the markings or sets of markings accurately coincides with and continues the pattern of the adjacent part of the limb. Even more striking

is the coincident disruptive coloration of the South American tree-frog Hyla leucophyllata and the East African Hegalixalus fornasinii. On the backs of these cryptic frogs is a central brown stripe, pointed in front and extending backwards to the end of the body. Stripes of the same colour occur on the inner sides of the hind limbs and on the sides of the body, the remainder of which is silvery white. When moving about, these frogs are, naturally, extremely conspicuous. While at rest, however, they can scarcely be recognised for what they are. This is because when the limbs are folded closely to the sides of the body, in their characteristic resting position, the silvery stripes on the exposed parts of the hind limbs coincide exactly with, and form extensions of, the silver stripes on each side of the back. At the same time, the dark lateral stripes, extending backwards from the nostrils, are continued along the outer parts of the front and hind legs, and cover the lower lids of the eyes. This striking colour scheme breaks up the entire form of the body into two strongly contrasted areas of brown and silver, neither of which looks anything like any part of a frog so that, although the animal may be a conspicuous object, its identity is completely disguised (Cott 1940).

Insects provide many striking instances of 'coincident coloration'. When the carpet moth Ligdia adustata is at rest, with its fore wings overlapping the hind wings and meeting along the axis of the body, the union of markings on one wing with the other are not particularly striking - although they strengthen the general disruptive coloration of the animal. In many other moths and butterflies, however, such as the orange-tip (Anthochoris cardamines), the oak beauty (Bison strataria), the scalloped oak moth (Crocallis elinquaria) and various tropical butterflies, the cryptic pattern on the underside of the fore wing is repeated beyond the margin of the hind wing.

Coincident disruptive patterns are very common among grasshoppers both in temperate and tropical regions. As with frogs, it is the enlarged hind legs that are most characteristic and especially liable to lead to recognition unless well disguised. Accordingly it is not surprising to find coincident stripes along the exposed parts of the legs and bodies of these insects. The stripes of species that live in grass are usually longitudinal while the grasshoppers of stony ground frequently show transverse stripes. Deceptive patterns of the kind we have been considering are particularly well displayed by fishes and reptiles. In many coral-reef fishes, for instance, disruptive bands of colour extend without a break from the body into the fins and tail. The angel fish *Pterophyllum scalare*) provides a striking example, as does *Dascyllus aruanus from the Philippines and Eques lanceolatus* from Florida (Cott 1940). Among snakes and lizards there are numerous species in which the outline of the body is broken up by series of light and dark bands. In addition, the

head often bears a disruptive stripe which extends uninterruptedly from the face and upper jaw across the mouth to the lower jaw.

The development of projections and processes that break up its outline are another means by which the body contour of an animal can be concealed. This is characteristic of many of the most perfectly camouflaged species. The outer wings of many cryptic butterflies and moths are often highly irregular and render the insects almost invisible when at rest. Deceptive modification of a similar kind occurs in various grasshoppers, leaf insects and plant bugs, and in the fins of the sea-dragon (*Phyllopteryx eques*) and the frog-fishes *Antennarius marmoratus* and *Pterophryne tumida* whose bizarre filaments blend perfectly with the sea weeds among which they live (Cott 1940).

Although the basic principles of disruptive coloration and dazzle patterns are clear, certain apparent anomalies occur. The black head, shoulders and limbs of the Malayan tapir (*Tapirus indicus*) are very conspicuous in a museum or zoo. But they contrast with the white body to break up the animal's shape and make it unrecognisable in the rainforests of Borneo, Sumatra and the Malay Peninsula. The significance of any form of adaptive coloration can only be considered in relation to the normal environment of its possessor. If the stratagem of the tapir is clear, that of the zebra is not. The zebra's stripes are frequently cited as examples of dazzle pattern but, perhaps more than in any other case of apparent disruptive coloration, their exact function has continually been questioned and disputed over the years (Cloudsley-Thompson 1984). Fourier analysis of their stripes, however, shows spatial frequencies in the pattern that are unlikely to be present so strongly in the natural background. When the hars is chased or startled, the conspicuous striped pattern may make it easier for zebras to recognise others in the panic of the moment (Godfrey *et al.* 1987), but this is by no means certain.

EYE STRIPES

On account of its regular shape, very ferw natural objects are more conspicuous than the vertebrate eye. Indeed, it is a mark by which predators would readily detect camouflaged prey, Unless it were well concealed. Many fishes, amphibians, reptiles, birds and mammals have eyes with black, staring pupils which require special treatment if they are not to prejudice the success of the whole colour scheme of the animals. One of the methods most commonly used is to conceal the eye by means of a black, coincident disruptive line or eye stripe. In the common frog (*Rana temporaria*), for example, a blackened stripe, level with the top of the pupil, extends over the iris and continues across the skin at the side of the head. This disguises the eye by incorporating it into the eye stripe.

Similar coincident eye stripes appear in a variety of other animals. They are especially common in fishes and snakes, being incorporated in the general disruptive patterns of the body. In the angel-fish (*Pterophyllum scalare*) there are two long black vertical stripes running across the body into the fins and a smaller anterior stripe passing through the eye. The angel-fish is a very slow swimmer, spending most of its time suspended almost motionless in mid-water where disruptive coloration enables it to escape detection. It is particularly inconspicuous when swimming among long strands of water weed and aquatic rushes (Norman 1975).

The garfish (Lepidosteus platystomus) provides an almost perfect example of eye camouflage. The front of the body is a uniformly sandy colour against which the round, jet-black pupil would be extremely conspicuous were it not camouflaged. The colour of the iris matches that of the head so that the orbit blends with the rest of the body but, in front of and behind the pupil, it is crossed by a black horizontal ribbon of pigment, exactly the same width as the pupil, which continues forward until it fades to a narrow point in the snout. The posterior extension of this eye stripe, on the other hand, becomes gradually wider and fainter in colour, until it merges into the general coloration of the body. Not only is the pupil thus concealed, but the whole circle of the eye is disrupted (Cott 1940, Edmunds 1974).

Snakes and lizards present many excellent examples of eye stripes which not only protect them from enemies but also help them to surprise their prey. In some, such as the slender arboreal vine-snake (Oxybelis acuminatus), the upper surface of the body is darker than the ventral, a black stripe passing across the centre of the eye. In others, although there is no distinctive stripe, the eye is obscured by the general disruptive blotches of pigment that cover the entire body.

Eye stripes are to be found in many cryptic birds including the ringed plover (Qaradrius hiaticula), whimbrel (Numenius phaeopus), woodcock (Scolopax rusticola) and turnstone (Arenaria interpres). They are less common among mammals although they can be seen in the southern African gemsbok (Oryx gazella) and other antelope, as well as in the vizcaca (Lagostomus maximus) of the Argentine pampas (Cott 1940, Edmunds 1974).

While the function of most eye stripes is mainly concerned with concealment, the birds which possess them are frequently those that feed on fast moving prey. Since the eye stripe normally passes from the eye to the beak, it could also act as a sighting line to increase the chances of catching active prey successfully

(Cloudsley-Thompson 1980). In grasshoppers and other animals where the stripes do not pass from the eye to the mouth, their function can only be one of camouflage.

MATERIALS FOR DISGUISE

Many of the defences found in the animal kingdom serve their possessors in more ways than one. A wide variety of different kinds of animals camouflage their bodies with materials taken from their environments. The sticks, pebbles or sand grains with which various species of caddis-fly larvae clothe their bodies have a dual function. Not only do they disguise their possessors but, at the same time, they make them distasteful to many potential predators. Even so, several species of fishes rely on caddis larvae for their food, so there must be heavy selection on the animals to build effective shelters. Trout eat caddis-flies in all stages and, if they cannot suck or blow the larva from its case, they will swallow it, case and all. Salmon have been found with large caddis cases (*Phryganea spp.*) in otherwise empty stomachs.

The terrestrial equivalent of caddis cases are constructed by the larvae of some of the bag-worm moths (Psychidae). These build protective cases of silk to which twigs, leaves and fragments of vegetable matter may be attached. They do not make a new case at every moult, but enlarge the original one as they grow. During moulting periods they anchor their cases to a leaf or the bark of a tree and close up the entrance. The female is flightless, and remains safely within the larval case after pupation. Pupae of the acacia bag-worm (Auchmophila kordofensis) of the African Sahel savanna inhabit very tough silk cases which are not only difficult to tear open, but also look very much like the seed-pods of the trees on which they hang (Cloudsley-Thompson 1968).

Many other kinds of insects conceal themselves with adventitious material. Although some of them are predatory, they would otherwise attack them. For instance, some lace-wing (Chrysopa spp.) larvae cover their backs with dead ants and, if these are removed, quickly replace them with others. Other lace-wing larvae, which feed on woolly alder-aphids, cover their backs with waxy material taken from the prey. This is loosely attached to the long bristles on their backs and results in astonishingly effective concealment. If the wax is removed with a paint brush, however, the lace-wing larvae are immediately attacked by the ants that normally guard the aphids, and dragged away. As soon as they have fixed more wax on their backs, however, they are ignored by the ants (Eisner et al. 1978). The wax must therefore serve additionally to deter ants from attacking the larvae.

Many marine animals, such as amphipods (Atylus spp.) and the crab Hyas araneus, cover themselves with sea-weed and, if moved into a new environment, promptly change their disguise so that they cannot be detected. A well-known example of adventitious disguise is the sponge-crab (Dromia vulgaris) which carries a sponge on its back. This not only disguises it, but makes it unattractive to otherwise dangerous predators. Many other crabs and molluscs have sea-weed, barnacles or hydroids growing on their backs (Yonge 1949). There is even a scorpion fish in Indian waters whose camouflage consists of an hydroid, which apparently lives nowhere else in the sea, attached to its body.

Perhaps the most extreme instance of the use of materials for disguise, however, is found among various weevils that live in the high altitude moss forests of New Guinea, and grow veritable gardens on their backs and legs. In these, there are to be found various species of algae, fungi, lichens, mosses and liverworts, sprouting from specially modified pits, surrounded by stout hairs, on the bodies of the beetles. Furthermore, like real gardens, the minute shrubberies are inhabited by a number of pests, including bacteria, Protozoa, nematode worms, rotifers or wheel-animalcules, and beetle-mites. This represents the ultimate in camouflage, and it is not surprising to find it in rain-forest, the oldest and most complex of the world's terrestrial biomes, in which natural selection between competing species has been operating for millions of years (Gressitt 1969, Hinton 1973).

DEFLECTION OF ATTACK

I once kept a number of Ghanian scolopendromorph centipedes in a glass vivarium containing moist humus. During the day they buried themselves but, at night, they would emerge from their hiding places and wander about looking for food. One evening, I noticed that the humus had become rather dry so I sprinkled water on it. A few drops fell on the centipedes, which had already emerged from their retreats. The falling water created a tremendous disturbance among them and, as they darted for cover, one of the animals dropped a back leg wich lay squeaking on the humus. The sound was audible from a distance of over a metre and persisted for about 40 seconds, until all movements of the leg had ceased. Subsequent experiments showed that sound production does not take place in attached legs, but only in the back pair after autotomy or self-amputation. The creaking sounds that accompany the movements of the autotomized limb are doubtless anadvantage to its former possessor, and distract the attention of an enemy even more than would the spontaneous movements of a silent leg (Cloudsley-Thompson 1960).

The long-legged scutigeromorph centipedes are also known to autotomize their legs when attacked. A vigorous contraction and relaxation of the muscles of the severed limb then takes place, accompanied by loud creaking sounds, which are produced by detached legs only. As they leap about, squeaking, they detract an enemy's attention from their owner, who slips away unobserved (Annandale, Brown and Gravely 1913, Lewis 1981).

Autotomy is usually practised as a form of self defence. I can well remember my dismay, as a child, on catching a lizard which promptly escaped, leaving only a wriggling tail in my grasp. At the time I was upset because I thought I had injured the lizard but, in fact, this was not the case. A lizard can break off its tail at will by muscular contraction but normally would only do so if it were seized by a predator. Not only does the severed tail tear off in the enemy's mouth, but the contraction of its muscles causes it to wriggle, thereby distracting the predator's attention while the lizard makes its escape (Arnold, 1978). Many other animals, in addition to lizards, are able to break off a part of the body when they are attacked, thereby distracting the attention of the aggressor.

Animals that do not autotomize parts of the body, nevertheless often have deflection marks which divert the attack of enemies from more to less important parts of the body. For instance, butterflies with eye-spots on their wings sometimes escape the attacks of birds by employing this ruse (Poulton 1890). The position of the spots themselves, which are commonly on the hinder margins of the back wings, is significant. Butterflies with these markings are quite often found with V-shaped imprints beside the eye-spots, showing how these have allowed them to escape with their lives (Carpenter 1941). Many predators make their initial strike at the head of the prey and several species of butterfly do not restrict themselves to eye-spots on the wings but actually have false heads at the tips of their hind wings well away from their true heads. The impression of a head is given by the antenna-like extensions of the tips of the hindwings, which are moved up and down after the butterfly has alighted, in the way that an insect's antenna often are, while the real antennae are kept still (Edmunds 1974).

Professional biologists have frequently described how they have been deceived by deflection marks and the displays that are associated with them. It is therefore not surprising that predatory animals, should also be misled. Sometimes, however, deflection marks have become so dramatic that they function as bluff and intimidate aggressors by their startling 'deimatic' effects. Again, mimicry may also be involved since genuinely poisonous or otherwise formidable animals have warning displays which predators learn, or instinctively avoid. Harmless species

cash in on this by displaying to predators in a similar way. This shows the complex interactions that may be exposed when one tries to unravel the deceptions that permeate the world of nature.

CONCEALMENT OF THE YOUNG

Eggs and young animals are particularly vulnerable to predatory enemies. Unable to escape by flight, they must frequently resort to disguise and deception if they are to escape unwelcome attention. The disruptive coloration of the eggs and young of the ringed plover and of the stone curlew have already been mentioned in this context. Even birds conspicuous as adults frequently have cryptic young. The lapwing is a familiar example. In contrast, the eggs of birds that nest in the protection of tree holes are invariably white and the hatchlings are never camouflaged.

Some birds construct elaborate nests and shelters for their eggs which, as everybody knows, may be extremely well concealed by the type of material used for their construction. Chaffinches (Fringilla coelebs), for instance, build their compact nests fairly low in trees and bushes, but these are so well camouflaged as to be almost invisible. A nest of lichen and moss wedged in the fork of a lichen-clad tree trunk will scarcely attract notice. Some warblers build even more elaborate nests, placing neatly woven structures between the stems of grasses or reeds. These are often cup-shaped, purse-shaped, or domed with a small entrance at the side. More remarkable is the nest of the related Indian tailor-bird (Orthotomus sutorius) inside the fold of a large hanging leaf whose edges are sewn together with plant fibres. The eggs of warblers are almost all white, buff; or greenish with fine spots.

The weavers of Africa build elaborate suspended nests, beautifully woven from vegetable fibres. These nests are often attached to the tips of twigs or palm frondsquite beyond the reach of snakes and other enemies, whose weight would prevent them from reaching the eggs. Such nests are often quite conspicuous, but since the eggs they contain are completely hidden from view, they may not appear particularly interesting to would-be predators. Weaver bird nests are frequently sited over water, which provides additional security, or very close to the nests of wasps, or of large, fierce birds, or to human habitations (Forsyth and Myiata 1984).

Birds are not the only animals to conceal their eggs or young. Many reptiles bury their eggs in the ground. Female sea turtles come ashore, often at night, on remote sandy beaches and with their flippers, excavate craters in the sand above the high tide level. Sometimes trial nests are dug and abandoned before the final site is selected. The eggs are finally covered over and well concealed before the female

returns to the sea where the male has been waiting for her. Land tortoises such as the American desert tortoise *Xerobates (Gopherus) agassizii*, sometimes urinte over their nesting sites so that the odour of their eggs is disguised by the evil smell produced in this way (Patterson 1971).

Crocodiles and alligators build nests for the protection of their eggs. The female either covers her eggs with sand, or hides them in a nest of plant debris. The eggs themselves are hard-shelled with a maximum length of about 9 cm (3.5 in). The mother Nile crocodile (*Crocodylus niloticus*) guards her nest, without feeding, through the 13 weeks of incubation. At the time of hatching, the babies make croaking sounds inside the eggs. When the mother hears these, she digs them up. If she did not do so, the young could not escape because the nest material gest so very hard as it dries. The mother crocodile defends her new-born young, and leads them down to the water, as ducks do. Sometimes she even takes them in her mouth and carries them to a safe place where the water is shallow and she can guard them from enemies (Shine 1988).

The king cobra (*Hamadryes hannah*) is not only the world's longest poisonous serpent, reaching a length of more than 5.5 m, but the female is the only snake known to build a nest out of vegetation, which she piles up with coils of her body. Like the Indian cobra (*Naja naja*), both female and male king cobras guard their hidden eggs aggressively (Shine 1988).

The young of some mammals are born, hidden in burrows. Others come into the world endowed with cryptic colours and behaviour. Marsupial babies are born in a relatively undeveloped state and at once climb into the safety of their mother's pouch, they remain safely hidden from the hostile outside world.

Every form of deception practiced among vertebrates is paralleled in the invertebrate world, and there are many others there that are unique. Some insect eggs are disguised as seeds, others are conspicuous and distasterful. The young of the frog-hoppers secrete themselves in a forthy substance, commonly termed 'cuckoo-spit', while the larvae of some of the crane flies of tropical America secrete quantities of hygroscopic protein which absorbs water vapour, swells up around the larva and makes it look like a rain drop about to fall from the tip of a leaf. Some of the sand-digging wasps that lay their eggs in holes in the ground go so far as to dig a large dummy burrow off the side of which the true burrow leads by a small hole. Any enemy that might investigate the wasps' burrow is likely to explore the empty dummy burrow and fail to notice the inconspicuous entrance leading to the eggs (Hinton 1955).

CAMOUFLAGE FOR OFFENCE

Camouflage is used by carnivorous animals for offensive purposes, just as it is used by herbivores for defence. Not all carnivores are camouflaged, of course, but predators that hunt active prey frequently depend upon surprise to catch it. The white coat of the polar bear (*Thalarctos maritimus*) enables it to stalk seals in a dazzling environment of ice and snow. If it were dark brown, like its relatives of warmer climes, it would stand little chance of approaching undetected, and its prey would quickly escape into the sea. Tigers (*Panthera tigris*), too, are notoriously difficult to distinguish in their normal environment of yellow grass; and the same is true of leopards (*P. pardus*). When the strong sunlight is dappled with patches of shade, the leopard's spots blend with and merge into the background. Fourier analysis of the stripes of the tiger shows that the spatial frequency is similar to that of its background (Godfrey *et al.* 1987).

The bright colours of the larger cats are highly cryptic in dry bush where they disrupt the outline of the body so that it becomes invisible to potential prey. moreover, since mammalian herbivores lack colour vision, the disruptive effect may be enanced at the expense of colour resemblance. Predatory animals thus avoid detection by their prey using the same devices that are employed by herbivores to escape notice. These include colour resemblance, obliterative shading, disruptive coloration, coincident patterns, camouflage of the eye and special deceptive.

Polar bears remain white throughout the year, but animals that live less close to the North Pole may have to change colour at different seasons. In summer, when the snow melts, the Arctic fox (Alopex lagopus) and ermine (Mustela erminea) lose their white coats and acquire dull brown or slate-coloured hairs which allow them to remain inconspicuous against a background of exposed rock and soil. The ermine is a stoat whose winter dress is entirely white save for the black tip of the tail. As a rule, stoats in Britain do not go white, or else go partly white - it depends on local temperatures. On Ben Nevis, they remain white throughout the year. Arctic predators which have no special need for concealment, such as the wolverine or glutton (Gulo gulo) and the sable (Martes zibellina), remain dark brown throughout the year. The sable lives and hunts its prey among fir trees, where its rich brown coat harmonizes with the bark, while the glutton is exclusively nocturnal and partly a carrion feeder (Cott 1940). Another predator to which inconspicuousness undoubtedly is useful when hunting, is the snowy owl (Nyctea scandiaca). This splendid bird of the far north is largely dependent upon lemmings for food, hunting them with silent flight during the short days, of winter and the long sunlit nights of summer.

In order to close in on its unsuspicious prey, a predatory animal frequently needs to approach slowly and with extreme stealth, taking elaborate precautions to reduce visible movement. We see this when a member of the cat family stalks its prey or a john dory (*Zeus faber*) stalks the smaller fishes on which it feeds. During these manoeuvres, the excessively thin body renders the dory inconspicuous as it edges its way slowly forwards until it is close enough for the protrusible jaws to shoot forwards and engulf the prey.

Most predators achieve success by means of a stealthy approach and the use of cover. The big cats must get close enough to be able to reach their prey with a short charge of lightning speed: they lack the stamina of members of the dog family which are able to chase prey until it is exhausted. At the same time, it would be useless to be camouflaged visually if a predatory animal were to disclose its presence by making a noise. Silence reaches its greatest development in the stalking movements of a leopard or tiger, and in the flight of an owl!

Predatory animals are not restricted to the use of simple camouflage as the means of deceiving prey. An element of surprise is often the vital component of a successful attack and this can be achieved in many different ways. Some carnivores escape recognition by mimicking leaves or sticks, but whether the function of this is aggressive or defensive is not always clear. Consider the American vine-snake (Oxybelis acuminatus) whose eyes are so well concealed by a coincident disruptive pattern. On account of its extraordinary slenderness combined with a grey-brown body colour splashed with blotches of silver, this arboreal snake counterfeits in remarkable detail the appearance, texture and form of a liana, the striking resemblance to which is enhanced by its habit of resting with the fore part of the body stretched forward horizontally and held motionless in space - apart from occasional swaying movements as though the liana had been caught by the wind (Bellairs 1969). The concealment is so good that the vine-snake can have little difficulty in deceiving the birds, lizards and other snakes on which it feeds. At the same time, however, it is invisible to potential enemies and can dart away with remarkable speed when alarmed.

The vine-snake has its counterparts in the tropical forests of Africa and Asia. These include the African bird-snake (*Thelotornis kirtlandii*) and the green mamba (*Dendraspis angusticeps*), both of which practice a similar mode of life (Ward 1979). In south-eastern Asia the same role is played by species of *Ahaetulla* (=Dryophis) whose head may be so elongated that it terminates like the sharpened load of a pencil. These are also leaf-green reptiles, but the skin between the scales is black. There is a startling effect when the snake is threatened, however, because

the body is then distended by inhalation and the green scales appear like jewels studded in a necklace while the interior of the open mouth appears black as if it were saturated with ink (Ditmars 1944).

A crocodile or alligator, lying motionless near the edge of the water, can easily be mistaken for a drifting log (Ward 1979). With only its knob-like eyes above water, it stalks its prey without making a ripple. Edging in, unobserved, the crocodile suddenly shoots forward and grips the leg or muzzle of a drinking animal, or knocks it into the water with a blow from the powerful tail. By looking like small logs, however, baby crocodiles may escape the attentions of fish eagles (Cuncuma vocifer), herons and other predatory birds (Cott 1961).

Some predators employ adventitious materials which hide them from their prey. For example, wide-mouthed toads of Brazil (Ceratophrys cornuta) hide in vegetation or throw lumps of soil over their backs and lie thus in ambush, waiting for some unfortunate creature to walk into their enormous mouths. The combination of burrowing habits and adventitious concealment reaches the limit of perfection among trap-door spiders, whose burrows are concealed by lids that exactly fit the entrances to their holes and are covered with fragments of moss or lichen from nearby.

There can be few carnivorous animals that do not have any predatory enemies, so it is often difficult to be certain whether the function of disguise is primarily offensive, defensive, or both. In the case of crab-spiders (Thomisidae) which change colour to match the flowers on which they are hiding, however, the function is clearly one of defence. When photographed by ultra-violet light they are quite conspicuous. Since the vision of insects, unlike that of vertebrates, extends into the ultra-violet, it must be assumed that the camouflage of crab-spiders is effective only against lizards, birds, and other predatory enemies, and does not function to hide the spiders from their insect prey (Cloudsley-Thompson 1980. Hinton 1973).

By the use of almost invisible webs, many spiders are able to trap flying prey which fail to discern the slender threads of the net spread before them. Sometimes the spider may lurk in wait, hidden beneath a leaf at the edge of the web, whence it detects the arrival of a meal through the vibrations of the web or, as previously mentioned, may disguise itself from both enemies and prey while it rests on the web. Again, the disguise has probably evolved mainly as a defence against predators such as lizards and birds.

Mimicry has not been discussed in this article, partly because it is such a vast subject that it would require separate treatment (Wickler 1968). Furthermore, examples of mimicry are not always readily apparent, whereas camouflage can be

demonstrated almost everywhere and at all seasons of the year. It provides one of the most striking examples of the effects of natural selection.

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بعض مظاهر التمويه في الحيوانات

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التمويه هي الطريقة الرئيسية التي تستطيع بها بعض الحيوانات المعرضة للإفتراس من الهرب من أعدائها . ويمكن تجنب إنتباه الحيوانات المفترسة بواسطة محاكاه شيء غير صالح للإفتراس مثل .. ورقة شجر أو حبة نبات .

ويتم الإختفاء من الأعداء بواسطة ألوان الحيوانات التي تشابه البيئة العامة وإلقاء الظلال المضادة والشفافية والألوان المتقطعة المتطابقة وكذلك الزوائد التي تقطع خط الجسم الخارجي وتميل عيون الفقاريات إلى أن تكون جلية تماما إلا إذا شابتها خطوط سوداء . كما يمكن إستخدام مواد نباتية للتنكير أو لجعل الحيوان الذي يحملها ذا مذاق غير مستساغ للحيوان المفترس .

وأخيراً يمكن إستخدام أسلوب التمويه والتنكير في الهجوم كما في الدفاع . ولقد تم عرضنا أمثلة عديدة من أساليب التمويه والتنكر .