= Adaptive Coloration in Animals =

Adaptive Coloration in Animals is a 500 @-@ page textbook about camouflage , warning coloration and mimicry by the Cambridge zoologist Hugh Cott , first published during the Second World War in 1940 ; the book sold widely and made him famous .

The book 's general method is to present a wide range of examples from across the animal kingdom of each type of coloration , including marine invertebrates and fishes as well as terrestrial insects , amphibians , reptiles , birds and mammals . The examples are supported by a large number of Cott 's own drawings , diagrams , and photographs . This essentially descriptive natural history treatment is supplemented with accounts of experiments by Cott and others . The book had few precedents , but to some extent follows (and criticises) Abbott Handerson Thayer 's 1909 Concealing @-@ Coloration in the Animal Kingdom .

The book is divided into three parts : concealment , advertisement , and disguise . Part 1 , concealment , covers the methods of camouflage , which are colour resemblance , countershading , disruptive coloration , and shadow elimination . The effectiveness of these , arguments for and against them , and experimental evidence , are described . Part 2 , advertisement , covers the methods of becoming conspicuous , especially for warning displays in aposematic animals . Examples are chosen from mammals , insects , reptiles and marine animals , and empirical evidence from feeding experiments with toads is presented . Part 3 , disguise , covers methods of mimicry that provide camouflage , as when animals resemble leaves or twigs , and markings and displays that help to deflect attack or to deceive predators with deimatic displays . Both Batesian mimicry and Müllerian mimicry are treated as adaptive resemblance , much like camouflage , while a chapter is devoted to the mimicry and behaviour of the cuckoo . The concluding chapter admits that the book 's force is cumulative , consisting of many small steps of reasoning , and being a wartime book , compares animal to military camouflage .

Cott 's textbook was at once well received , being admired both by zoologists and naturalists and among allied soldiers . Many officers carried a copy of the book with them in the field . Since the war it has formed the basis for experimental investigation of camouflage , while its breadth of coverage and accuracy have ensured that it remains frequently cited in scientific papers .

= = The book = =

= = = Approach = = =

Adaptive Coloration in Animals is a 500 @-@ page book , 10 by 7 inches (250 by 180 mm) in its first edition . It was published by Methuen (in London) and Oxford University Press (in New York) in 1940 . It is full of detailed observations of types of camouflage and other uses of colour in animals , and illustrated by the author with clear drawings and photographs . There is a coloured frontispiece showing eight of Cott 's paintings of tropical amphibians . The book has 48 monotone plates and several illustrations .

Cott 's method is to provide a large number of examples , illustrated with his own drawings or photographs , showing animals from different groups including fish , reptiles , birds and insects , especially butterflies . The examples are chosen to illustrate specific adaptations . For example , the fish Chaetodon capistratus is described as follows :

this species had the habit of swimming very slowly tail first : but when disturbed it darts rapidly off to safety in the opposite direction ... C. capistratus adopts the same tactics ... [This fish] is of particular interest in that the real eye is obliterated and a false eye substituted in one and the same animal .

Cott was well aware that he was publishing in wartime . There are , as Julian Huxley remarks in his ' Introduction ' , references throughout the book to the human analogues of animal camouflage and concealment . For example , in the section on ' Adaptive Silence ' , the kestrel is said to " practise dive @-@ bombing attacks " , or " after the fashion of a fighter ' plane " to fly down other birds ,

while " Owls have solved the problem of the silent air @-@ raid " ; Cott spends the rest of that paragraph on the " method which has recently been rediscovered and put into practice " of shutting off a bomber 's engines and " gliding noiselessly down towards their victims " at Barcelona in the Spanish Civil War . In the concluding chapter , Cott explicitly states " The innumerable visible devices used .. in peace @-@ time and in war @-@ time .. are merely rediscovered .. applications of colour that have already reached a high .. degree of specialization and perfection .. in the animal world " , mentioning predator @-@ prey relationships , sexual selection and signalling to rivals . He then compares the " hunting disguises put on .. as a means of approaching , ambushing or alluring game , and the sniping suits , concealed machine @-@ gun posts , and booby traps " with the camouflage of animal predators ; and similarly he compares " protective disguises " with the " photographer 's hide and the gunner 's observation post . " In the same section , Cott compares intentionally visible signs with animal warning colours : " The policeman 's white gloves have their parallel in the white stripes or spots of nocturnal skunks and carabids . The Automobile Association has adopted a system of coloration [black and yellow] whose copyright belongs by priority to wasps and salamanders . "

= = = Structure = = =

The book addresses its subject under three main headings : concealment , advertisement , and disguise .

= = = = Part I : Concealment = = = =

The methods by which concealment is attained in nature

Cott sets out his view that we have to be re @-@ taught how to see , mentioning Ruskin 's " innocence of the eye " . He argues that camouflage should , and in animals actually does , use four mechanisms : colour resemblance , obliterative shading (i.e. countershading , the graded shading which conceals self @-@ shadowing of the lower body) , disruptive coloration , and shadow elimination .

Chapter 1 . General colour resemblance .

Cott gives many examples such as a table of 16 species of green tropical tree @-@ snakes .

Chapter 2 . Variable colour resemblance . Caterpillars and pupae (as in Poulton 's famous experiment) are coloured to match their environment . Mountain hares change colour in winter ; many fish , cephalopods , frogs , and crustacea can change colour rapidly .

Chapter 3 . Obliterative shading .

Following the artist and amateur naturalist Abbott Handerson Thayer , Cott explains countershading with diagrams , photographs of models and examples of real animals . He shows how helpful it would be for military camouflage with drawings of gun barrels .

Chapter 4 . Disruptive coloration .

Cott argues with diagrams , drawings , photographs and examples that animals are often extremely effectively disruptively patterned . He analyses the component effects of disruption , including " differential blending " and " maximum disruptive contrast " . Cott 's figure 7 is a set of nine drawings , arranged as a 3x3 table . On the left is an animal 's outline in grey tone against a differently coloured background . In the centre , the same animals are now disruptively patterned against the same plain backgrounds . On the right , the disruptively patterned animals are shown against realistic broken backgrounds containing vegetation or rocks . Cott explains

The simplified diagrams in Fig . 7 illustrate the value and effectiveness of maximum disruptive contrasts better than any verbal description ... On looking at these drawings from a little distance , it will be seen that the conspicuous patches operate most efficiently in distracting attention from the form of the animals wearing them . By sheer force of their brightness , or blackness , or contrasts , they dominate the picture presented to the eye , apparently destroying their form ...

Cott goes on to explain that the right @-@ hand drawing shows the effect " of broken surroundings in further blending and confusing the picture " , observing that this is the closest to what is seen in

nature . His readers are invited to look first at the right @-@ hand images to gain an idea of the power of " these optical devices " as camouflage , putting off the moment when the animal is actually recognised .

Chapter 5 . Coincident disruptive coloration .

Animals such as frogs are patterned so that when they are at rest with legs tucked in , their outline is powerfully disrupted with markings that seem to flow across body and leg boundaries . Eyes too are often hidden in stripes .

Chapter 6 . Concealment Of the shadow .

Cast shadows give away even well @-@ camouflaged animals . Many animals therefore take care to minimise shadow , by lying down , with flattened bodies , or with fringes . Some hawkmoth caterpillars have false shadow patterns to suggest they are parts of other objects .

The function of concealing coloration in nature

Chapter 7 . Concealment in defence , mainly as illustrated by birds .

Cott considers how effective camouflage is as an adaptation , such as in incubation and rest (sleep) in birds . For instance nightjars are nocturnal , and rest , well camouflaged , on the ground during the day .

Chapter 8 . Concealment In offence .

Cott describes the care that predators take when approaching prey , minimizing visible movement and scent , the use of cover for ambush , and " adaptive silence " .

Chapter 9 . Objections and evidence bearing on the theory of concealing coloration .

In this chapter Cott discusses various objections to the adaptive (evolutionary) nature of camouflage , and provides evidence to dismiss them . Some are " based upon such obvious fallacies that they hardly deserve serious consideration . "

Chapter 10 . The effectiveness of concealing coloration .

Cott describes simple experiments such as that fish that have changed colour to match a pale background survived better (64 % to 42 %) on such a background than fish which had not . He also quotes some anecdotal observations on wild animals with similar but not quantified results .

= = = = Part II : Advertisement = = = =

The methods by which conspicuousness is attained in nature

Chapter 1 . The appearance and behaviour of aposematic animals .

Animals that are genuinely distasteful (aposematic) boldly advertise themselves in black , white , red , and yellow . They are often " sluggish " , not running from predators ; gregarious ; and diurnal , since warning displays only work if they can be seen " by potential enemies " .

Chapter 2 . Warning displays .

Aposematic animals often have (honest) threat displays ; edible prey sometimes have (bluffing) startle displays . For example the frilled lizard , Chlamydosaurus kingii , is illustrated in a drawing by Cott , with its tail raised over the body , stretched up on all four legs , mouth wide open , and frills out both sides of the head , making it a startling sight .

Chapter 3 . Adventitious warning coloration .

Some marine animals select aposematic materials as coverings , not only as camouflage . Some birds nest near wasps ' nests .

Warning coloration in relation to prey

Chapter 4 . The nature and function of warning coloration , as illustrated by the mammalia .

Prey like porcupines have warning colours , make noise , and attack predators (even leopards) .

Chapter 5 . The Protective Attributes Of Aposematic Animals In General .

Evidence is given that conspicuous animals such as caterpillars really are distasteful . Animals with actual poisons are discussed , and how these are secreted , used in bites and stings , or kept to make the animal bitter tasting .

Chapter 6 . The relation between warning colours and distasteful attributes .

Various kinds of evidence are presented for aposematism .

Chapter 7 . The effectiveness of protective attributes associated with warning colours .

Experimental evidence is presented that insects with warning colours are rejected by predators .
Warning coloration in reference to predatory enemies
Chapter 8 . Experimental evidence that vertebrate enemies learn by experience .
Experiments by Cott show that toads learn to avoid eating stinging bees .
Chapter 9 . Evidence of selective feeding by vertebrate enemies in a state of nature .
Evidence from wild birds and toads demonstrates preferences for particular prey .

= = = = Part III : Disguise = = = =

Special protective and aggressive resemblance
Chapter 1 . Special resemblance to particular objects .
Cott describes leaf @-@ like fish , chameleons , and insects , and other mimetic forms of camouflage . A liana @-@ like snake near Para (a haunt of Henry Walter Bates in Naturalist on the River Amazons) 160 times as long as it was thick is called " a revelation in the art of aggressive resemblance " .
Chapter 2 . Adaptive behaviour in relation to special cryptic resemblance .
Animals keep still , sway in the wind , or play dead to assist their camouflage . Poulton 's examples of twig @-@ like Geometridae caterpillars are praised . There are fine photographs of leaf insects , and Cott 's admired drawing of a poor @-@ me @-@ one or potoo , Nyctibius griseus , sitting on its nest mimicking a broken branch . Cott explains , in a section on " Special resemblances in relation to the attitude of rest "
This wonderful bird ... habitually selects the top of an upright stump as a receptacle for its egg , which usually occupies a small hollow just , and only just , large enough to contain it . ... the stump selected had thrown up a new leader just below the point of fracture ; ... the bird sat facing this in such a way that when viewed from behind they came into line and blended with the grey stem .
Chapter 3 . Adventitious Concealing Coloration .
Cott begins by citing Shakespeare 's Macbeth with " until / Great Birnamwood to the Dunsinane hill / Shall come against him " to introduce his chapter on the use of materials as camouflage . Animals from crabs to caterpillars are described .
Conspicuous localized characters
Chapter 4 . Deflective marks .
Cott describes markings that help to deflect attack , such as the eyespots of butterfly wings and the twitching cast @-@ off tails of lizards , both acknowledged to Poulton , as well as the distraction displays of birds such as the partridge mentioned by Gilbert White in his Natural History and Antiquities of Selborne .
Chapter 5 . Directive marks .
A selection of lures and deceptive markings are described . A large drawing depicts the deimatic warning display of a mantis , Pseudocreobotra wahlbergi with its spined forelegs raised and large spiral eyespots on its spread wings forming an image " suggestive of a formidable foe " . Other drawings depict the eyespots of fish such as Chaetodon capistratus , the four @-@ eye butterfly fish , which are " usually towards the tail end " and tending to direct attack away from the head .
Alluring and mimetic resemblances
Chapter 6 . Alluring coloration .
The bird @-@ dropping spider Ornithoscatoides decipiens , the flower mantis Hymenopus bicornis and other camouflaged hunters are described .
Chapter 7 . Mimicry : the attributes of mimics .
Cott follows Poulton in treating mimicry as basically the same as camouflage or " adaptive resemblance " . Batesian mimicry and Mullerian mimicry are compared . The behaviour of " Esquimaux seal @-@ hunters " and First World War Q @-@ ships are mentioned .
Chapter 8 . Breeding parasitism and mimicry in cuckoos .
The mimicry and behaviour of the European cuckoo , Cuculus canorus is analysed .

= = = = Conclusion = = = =

The final chapter confirms that " The force of the facts and arguments used in this work is cumulative in effect . " Many small steps of reasoning combine to show that " adaptive coloration ... has been ... one of the main achievements of organic evolution . " The book ends by comparing human artefacts and " natural adaptations " , both of which can have goals (recall the publication date of 1940 , early in the Second World War) including " the frustration of a predatory animal or of an aggressive Power " .

= = Reception = =

= = = Foreword = = =

Julian S. Huxley wrote a foreword (labelled ' Introduction ') which defends the Darwinian concept of adaptation , especially of colour (in animals) and within that frame of mimicry . He makes it clear that " in these last thirty years " (that is , from about 1910 to 1940) he believed that " experimental biologists " professed , even if they did not actually hold , " a radical scepticism on the subject of adaptations " , in other words about whether natural selection really could have created the enormous diversity of pattern and colour seen in nature . Huxley quoted the now long @-@ forgotten Aaron Franklin Shull 's 1936 Evolution which stated " These special forms [sexual selection , warning colours , mimicry and signalling] of the selection idea ... seem destined to be dropped , or at least relegated to very minor places in the Evolution discussion . " , and more sharply that " aggressive and alluring resemblance " (Huxley 's words) " must probably be set down as products of fancy belonging to uncritical times . " Huxley 's reply is simply

Dr. Cott , in this important book , has turned the tables with a vengeance on objectors of this type ... Had they taken the trouble to acquaint themselves with even a fraction of the relevant facts to be found in nature , they could never have ventured to enunciate such sweeping criticisms : their objections are a measure of their ignorance .

With objections dismissed , Huxley remarks that " Dr. Cott is a true follower of Darwin in driving his conclusions home by sheer weight of example , " observing that " Faced with his long lists of demonstrative cases , the reader is tempted to wonder why adaptive theories of coloration have been singled out for attack by anti @-@ selectionists . " Huxley also noted Cott 's " constant cross @-@ reference to human affairs " , and that it was good to know that Cott was applying his principles " to the practice of camouflage in war " .

Huxley concluded his introduction by describing Adaptive Coloration as " in many respects the last word on the subject " , upholding the great tradition of " scientific natural history " .

= = = Contemporary reviews (circa 1940) = = =

Reviewers had little to compare Adaptive Coloration with . The English zoologist Edward Bagnall Poulton , a Darwinian , had written a 360 @-@ page book , The Colours of Animals , fifty years earlier in 1890 , and he was able , at age 84 , to review Cott 's work in Nature on its appearance in 1940 , beginning with the words

This excellent work , eagerly awaited for many years , will be most welcome to naturalists , even , we may hope , to the few who have hitherto rejected the Darwinian interpretation which the author has here supported by a mass of additional evidence based on his own observations and those of very many others .

The ichthyologist Carl Leavitt Hubbs , reviewing the book for American Naturalist in 1942 , began

In this Neodarwinian epic Dr. Cott stamps himself as a true disciple of the master evolutionist . Indeed , he rivals Darwin in the thorough , objective and penetrating analysis of a major biological problem . An immense body of facts and interpretation , much of it original , has been judiciously considered and brought to bear on the question of the biological significance of coloration .

Hubbs notes that Cott is seeming concerned about the scarcity of experimental data for the survival

value of camouflage , and accordingly relies on Sumner and Isely 's " clear @-@ cut results " , but at once continues that Cott relies on " the general lore of natural history " . Hubbs also remarks on the " resurgence to Darwinian views " , referring to the scepticism about the power of natural selection among both geneticists of the time and to the Lamarckist views of Trofim Lysenko .

Hubbs observes that Cott is both an artist and a naturalist as well as a scientist : " In section after section , rivaling one another in fascination , this master of art and of natural history unfolds the biological significance of adaptive coloration in animals . " And Cott 's emphasis on disruptive patterning and (following Thayer) countershading clearly affected the reviewer : " Particularly impressive is the author 's treatment of " coincident disruptive coloration " , in which a ruptive mark crosses structural boundaries , so as to obliterate visually such ordinarily conspicuous parts as the eye and the limbs . Concealment of an animal 's ordinarily telltale shadow is also stressed " . Hubbs 's review ends " This book is the work of an artist , and it is a work of art . Every biologist with an interest in any phase of natural history or evolution should keep it at hand . "

" W.L.S. " , reviewing Cott in The Geographical Journal in 1940 , begins with " In this large and well @-@ illustrated volume the author discusses at length reason or reasons for the various colour patterns found in the animal kingdom . " The reviewer goes on " He has presented us with a vast number of facts and observations which are somewhat difficult to analyse . " However " W.L.S. " admits that disruptive coloration " is discussed at considerable length by Mr. Cott and many remarkable instances of it are considered in detail " . The review ends by mentioning that while biologists (of the 1930s) usually " reject the influence of Natural Selection in evolution , the facts of adaptive coloration as given in Mr. Cott 's work are a strong argument in its favour , and must be given due weight . This is what Mr. Cott claims to have accomplished in a volume which will certainly take its place as a most valuable contribution to zoological literature . "

= = = Looking back (after 2000) = = =

Peter Forbes , in his book Dazzled and Deceived , wrote that

Cott 's Adaptive Coloration in Animals must be the only compendious zoology tract ever to be packed in a soldier 's kitbag . The book also marks the apotheosis of the descriptive natural history phase of mimicry studies . Although Cott does report experiments on predation to test the efficacy of mimicry and camouflage , the book is essentially a narrative of examples plus theory .

Over 60 years after its publication , Adaptive Coloration in Animals remains a core reference on the subject . Sören Nylin and colleagues observe in a 2001 paper that

Adaptive coloration in animals has been a very active research field in evolutionary biology over the years (e.g. Poulton 1890 , Cott 1940 , Kettlewell 1973 , Sillen @-@ Tullberg 1988 , Malcolm 1990) , and one in which the Lepidoptera have always featured prominently as model species .

As a natural history narrative on what has become an intensely researched experimental subject , Adaptive Coloration could be thought obsolete , but instead , Peter Forbes observes " But Cott 's book is still valuable today for its enormous range , for its passionate exposition of the theories of mimicry and camouflage " . This width of coverage and continuing relevance can be seen in the introduction to Sami Merilaita and Johan Lind 's 2005 paper on camouflage , Background @-@ Matching and Disruptive Coloration , and the Evolution of Cryptic Coloration , which cites Adaptive Coloration no fewer than eight times , quoting his terms " cryptic coloration or camouflage " , " concealing coloration " , " background matching (also called cryptic resemblance) " , " disruptive coloration " , resemblance to visual background , and the difficulty a predator has to detect a prey visually .

Steven Vogel , in a review of Peter Forbes 's book Dazzled and Deceived (2009) , echoes Julian Huxley 's words of seventy years before (in his ' Introduction ') by writing

The zoologist Hugh Cott had the final word in Adaptive Coloration in Animals (1940) , a definitive synthesis of everything known about camouflage and mimicry in nature . Cott ruffled fewer feathers [than Trofim Lysenko or Vladimir Nabokov] , and his well @-@ organized and unfanatic ideas proved militarily effective , even under the scrutiny of improved techniques for target detection . Thayer ? s principles reemerged in more temperate and rational terms , and camouflage schemes

based on them survived both photometric analyses and enemy encounters . Biomimetic camouflage took its place as yet another technique in a sophisticated armamentarium of visual deceptions .

Camouflage researcher Roy Behrens cites and discusses Adaptive Coloration frequently in his writings . For example , in his Camoupedia blog , related to the book of the same name , he writes of Cott 's drawings of the hind limbs of the Common frog : " Reproduced above is one of my favorite drawings from what is one of my favorite books . " He continues " What makes these drawings (and the book itself) even more interesting is that Cott (1900 @-@ 1987) was not just a zoologist ? he was a highly skilled scientific illustrator (these are his own pen @-@ and @-@ ink drawings) , a wildlife photographer , and a prominent British camoufleur in World War II . " Still in 2011 , Behrens can write of Cott 's way of thinking , citing his words as models of clear and accurate explanation of the mechanisms of camouflage : " As he so aptly explained it , disruptive patterns work ' by the optical destruction of what is present ' , while continuous patterns work ' by the optical construction of what is not present . ' "

= = Publication history = =

Adaptive Coloration in Animals has been published as follows :
1940 , Methuen , Frome and London (printed by Butler and Tanner) . Foreword by Julian Huxley
1940 , Oxford University Press , New York
1941 , Oxford University Press , New York
1957 , Methuen , London (reprinted with minor corrections)
1966 , Methuen , London (reprinted with minor corrections)

= = = Primary = = =

This list identifies where in Cott 's book the quotations come from .

= = = Secondary = = =