Adaptive Coloration in Animals

HUGH B. COTT

Adaptive Coloration in Animals

HUGH B. COTT

M.A., D.Sc., F.R.P.S., F.Z.S.

Lecturer in Zoology and Strickland Curator
Cambridge University

WITH AN INTRODUCTION BY

JULIAN S. HUXLEY

METHUEN & CO LTD

36 ESSEX STREET · STRAND · LONDON WC2

INTRODUCTION

AMONG a certain section of experimental biologists, any time in these last thirty years, it has been fashionable and indeed almost a matter of professional conscience to display a radical scepticism on the subject of adaptations, especially colour adaptations, and most particularly mimetic adaptations. Upholders of the theories of protective and warning coloration and of mimicry have often been attacked as 'armchair theorists' (whereas they have in fact almost invariably been first and foremost field naturalists), insufficiently acquainted with modern work in genetics, which for some unexplained reason is held to do away with adaptive interpretations.

Thus, for instance, to cite but one recent author, A. F. Shull in his book on *Evolution* (1936) writes (p. 212):

> if the doctrine [of natural selection] can emerge minus its sexual election, its warning colors, its mimicry and its signal colors, the reaction over the end of the century will have been a distinct advantage. These special forms of the selection idea . . . seem destined to be dropped, or at least relegated to very minor places in Evolution discussion.

Elsewhere (p. 175) he states that the theories of aggressive and alluring resemblance 'must probably be set down as products of fancy belonging to uncritical times'.

Dr. Cott, in this important book, has turned the tables with a vengeance on objectors of this type. He has shown that it is they who are the armchair critics, or, one might say, the laboratory-bench critics. 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. Further, by applying optical and psychological principles, he has pushed the analysis of visual allæsthetic characters to a new level, and shown that many of them constitute adaptations of a quite unsuspected degree of refinement. Far from genetics in any way throwing doubt on their adaptive interpretation, the facts of cryptic, warning and mimetic coloration pose searching questions to the geneticist, and demand a recasting of many current views on the efficacy and mechanisms of selection.

This analysis is the most original part of Dr. Cott's book. With the aid of his own remarkable drawings and photographs, he demonstrates how nature—in this case via the operation of natural selection—employs the most elaborate

optical-psychological devices to enhance conspicuousness where conspicuousness is advantageous, to reduce it where obliteration is the biological aim.

Cases in which an unusual resting position is adopted provide beautiful evidence of his contentions. Counter-shading is reversed in fish which swim upside-down and caterpillars which rest inverted. Bark-haunting moths have their markings running parallel with the vertical cracks of the bark, whether they rest with body vertical or horizontal, with wings folded or expanded.

The correlation of behaviour and markings, indeed, as Poulton long ago pointed out, is one of the strongest supports for theories of adaptive coloration. Even if it were possible for a case-hardened sceptic to dismiss as accidental such isolated facts as the co-existence, in various stingless insects, of a resemblance to bees or wasps on the one hand and on the other of motions simulating stinging, and even of the protrusion of an imitation sting, the enormous array of less spectacular but equally significant correlations provided by Dr. Cott is overwhelming.

Dr. Cott is a true follower of Darwin in driving his conclusions home by sheer weight of examples. 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. As Dr. Cott observes, physiologists and geneticists do not deny that wings exhibit characters which make them suitable as mechanisms for flying, or that legs, beaks and teeth are adaptively correlated with mode of life.

A proper analysis, such as that undertaken in this book, demonstrates conclusively that optical-psychological principles promoting increase or decrease of conspicuousness in correlation with mode of life are just as effectively employed in animal coloration as are aerodynamic principles in the construction of flying animals. There is no more justification for denying the functional (and therefore adaptive) significance of the one than of the other.

Let it not be supposed, however, that the experimental approach has been neglected. Here again the anti-Darwinian critics of the theories of adaptive coloration seem not to have taken the trouble to acquaint themselves with the facts. The experimental data conclusively demonstrate that cryptic, warning and mimetic forms do in point of fact enjoy a degree of immunity from predators which constitutes a considerable selective advantage in the struggle for existence. Some of the recent work is especially convincing.

Another novel and interesting feature of this book is the constant cross-reference to human affairs. Dr. Cott shows how the same optical principles automatically utilized by natural selection in animal coloration have over and over again been employed deliberately and of set purpose by men to achieve the same effects. It is good to know that he has been called on to apply the principles he has studied to such good effect in animals to the practice of camouflage in war.

Adaptive Coloration in Animals is perhaps the most satisfactory book yet written on adaptation. It brings together great masses of data, from the field, the museum and the laboratory, analyses them in the light of established physical

and psychological principles, and deals satisfactorily with the methodological problem of establishing proof of their adaptive nature. It is a worthy successor to Sir Edward Poulton's *The Colours of Animals*, published nearly half a century ago. The one was a pioneer study, the other is in many respects the last word on the subject. It is very gratifying to see that one of the great traditions of British biology—the tradition of scientific natural history, in which the comparative treatment of patiently accumulated data is made to yield generalizations of first-class importance—is being so worthily upheld.

JULIAN S. HUXLEY

此为试读,需要完整PDF请访问: www.ertongbook.com

PREFACE

THERE are many ways of regarding living creatures. They appear very differently to different men. What we see in an animal depends both upon our outlook and experience. To the morphologist, it presents problems of structure and descent; to the systematist, it raises questions of relationship and classification; the embryologist interests himself in its development; the psychologist, in its behaviour; to the stock-farmer, it has market value; to the artist, beauty; to the naturalist, a place to live and a part to play in the world of life. Even within the confines of a specialized study, like that of animal coloration, the same wide differences in approach and outlook exist. Here the biochemist is concerned with chemical problems of pigmentation; the physicist, with the optics of structural colours; the geneticist attempts to analyse colour-characters in terms of heredity; the systematist traces in them an indication of relationship; the physiologist studies their functions in the body; the naturalist, their functions in the field.

In the interrelationships between animals of the same, or of different species—as between predator and prey, between rival males, or the opposite sexes, between parent and offspring, or between members of the group—characters which exert their influence from a distance, by sound, by sight, or scent, take a prominent place. To such characters Julian Huxley has applied the useful and comprehensive term Allæsthetic. In this volume I have intentionally confined myself to a special study of the various manifestations and functions of coloration in the interspecific relations of animals—that is to say, in the relations between predator and prey. Thus it will be apparent at the outset that auditory and olfactory characters have not been dealt with, except in so far as their mention may be relevant to my purpose; and that, on the other hand, I have excluded as beyond the scope of the present volume that large and important class of coloration-phenomena whose function has to do with intraspecific relations—coloration, in other words, used for threat by rival males, for courtship by members of the opposite sex, and for recognition, by members of the family, or flock.

One of the fundamental facts affecting living creatures is the interspecific warfare known to biology as the struggle for existence. Animals, like men, are beset by many and great dangers. The problem of self-preservation in the field is very real, very urgent, and often difficult enough to solve; but it is one with which all forms of animal life are faced. Broadly speaking, individual survival depends upon the satisfaction of two vital needs—security and sustenance. These are the two primary claims of life. In a world peopled with potential enemies and pregnant with hunger and the possibility of starvation, if an animal is to

survive, it must eat, and avoid being eaten. It is the old question of the relation between the aggressor and the victim of aggression, between hunter and hunted.

The very urgency of this central biological problem of self-preservation is reflected in the variety and specialization of nature's adaptive experiments in offence and defence, as it is also in the parallel inventions and contrivancies of man. Indeed, the primeval struggle of the jungle, and the refinements of civilized warfare, have here very much the same story to tell. In both realms we see the results of an armament race and an invention race, which has led to a state of preparedness for offence and defence as complex as it is interesting. In both, methods mainly similar are employed: we have the evolution of speed, on land, in the air, and under water, by pursuer and pursued; the employment of stealth and surprise, of deception and ambush; the display of warning signals and of alluring baits; the elaboration of smoke-screens, traps, nets, parachutes, of electrocution and booby-traps; the adoption of fossorial and nocturnal habits; the development of poison, and of deadly apparatus in the form of fangs or stings or arrows for its injection into the bodies of enemies or prey; the protection afforded by armour-plating, spines and barbed wire; the use of chemical warfare, which is practised, for instance, by certain insects; and of poison gas, by creatures like the skunk.

Among all these evolutionary achievements, perhaps none are more important, more widely used, and more highly developed, than those characters which serve to elude, to attract, or to deceive the eye, and so to facilitate escape from enemies or the pursuit of prey. Indeed, it is no exaggeration to say that the modification of outward appearance by visual characters, directed towards a seeing public, and serving either to facilitate recognition or to frustrate it, has been one of the main results attained in the evolution of the higher animals; and such characters comprise some of the most outstanding examples of adaptation in the whole field of biology.

In most spheres of modern warfare man has now, though in some cases only very recently, advanced far ahead of the so-called brute creation in his equipment for protection and aggression—in regard, for instance, to the development of armour and mobility, to the use of projectiles, and of devices such as the balloon-barrage and submarine-net (which in principle are gigantic spiders' webs), of smoke-screens (which are employed with effect by cuttle-fishes), and of delicate instruments like range-finders and sound-detectors. Yet, while there is the closest analogy between the needs for concealment and deception in nature and in war, in this sphere the coloration of animals has attained a degree of perfection far beyond the comparatively crude attempts at camouflage with which we are too easily satisfied—attempts which often neglect to make use of the very principles revealed in the coloration of innumerable snakes, caterpillars, birds, fishes and other organisms.

Because of recent developments in aerial warfare, and the ever-increasing part played by aircraft in military and naval operations of all kinds—for reconnaissance, photography, and bombing—camouflage has assumed to-day a new

and vital function, whose significance can scarcely be overstated. But we have lagged far behind nature, and have much leeway to make up before we can approach the efficiency attained by different forms of wild life in the field. We should do well, therefore, to follow advice from the Book of Job: 'But ask now the beasts, and they shall teach thee; and the fowls of the air, and they shall tell thee . . . and the fishes of the sea shall declare unto thee.'

A satisfactory system of classification, while primarily a matter of convenience, is nevertheless one of great importance to the serious study of any phenomena. Many of us had an early introduction to classification when, as children, we learned to play the game 'Animal, Vegetable and Mineral'. Now the phenomena of adaptive coloration likewise fall into three main classes, according to the visible results produced. I have accordingly divided the present work into parts devoted, respectively, to questions of concealment, of advertisement, and of disguise. The biological function of these elusive, attractive, or deceptive devices varies widely according to circumstance, Through reduced visibility, they may facilitate the capture of food, or escape from the aggressor. Through increased conspicuousness, they may serve as a warning, or as bluff, to potential enemies, or as an allurement to prey. Through deceptive or mimetic effects, they may mislead the observer as to an animal's whereabouts, attitude, or identity.

It would be great presumption for any one to attempt a book on functional aspects of animal coloration without acknowledging a deep debt of gratitude to Sir Edward Poulton, D.Sc., F.R.S., whose classical work on *The Colours of Animals* appeared just half a century ago. Whatever the subsequent developments of our knowledge in this field of natural history, Poulton's analysis and classification of the phenomena must remain the essential structure upon which others may build. The great array of facts which have since been accumulated are largely due to his untiring labours, and in the preparation of the present work I have time and again had occasion to refer to his writings. Reference has been made in the text to the original publications from which I have drawn examples and evidence.

Although such a study as this is somewhat specialized, it is nevertheless one bearing directly upon that central problem of biology—the mechanism of evolution. In this book I have been less concerned with the origin of adaptive coloration, than with its various manifestations and uses. Nevertheless, those who are more interested in questions of origin, than in effects and applications, will find assembled in these pages a body of facts and evidence from which they may draw their own conclusions. The theory of natural selection is to-day receiving support from a number of sources. One of these sources is the scientific study of natural history, and in particular of adaptive coloration. Indeed, in the light of modern knowledge, the claim may well be repeated and emphasized, which was made in 1898 by Poulton, when he wrote that 'the explanation of these deeply interesting facts, which form so fascinating and important a department of natural history in the tropics, is one of the most notable triumphs ever won by the great Theory of Natural Selection'.

In a book which deals, as this book deals, with optical principles and outward appearances, illustrations must take an important place, and I have spared no pains in the preparation of a series of photographs and drawings which will, I trust, materially add to any usefulness the work may possess. I have heard the view expressed that photographs do not provide reliable evidence as to the effectiveness of concealing coloration, since, it is argued, animals are more difficult to detect in the photographs than they would be in the field. Now this opinion does contain an element of truth when applied to some photographs—bad photographs. Every one has seen reproductions intended to illustrate some cryptic insect or bird, in which the creature remains unfound, not because of its cryptic coloration, but because the picture is technically deficient—lacking in clarity of outline, or in range of tones, or in scale, or because it is badly printed on vile paper. On the other hand, with illustrations of good quality—and in these days of ultra-rapid sensitive materials and ultra-precise cameras there is really no excuse for indifferent photography—the reverse is certainly true. In the sphere of aerial reconnaissance, it is the camera, and not the observer, which yields the exact data so necessary for the detection of camouflage. The photographic record is more accurate and discriminating than the retinal record, and camouflage is more readily spotted from the former than from the latter. Moreover, the limited field over which the eye must explore greatly facilitates the detection in a print of a cryptic insect which in nature may well escape observation since not even its approximate whereabouts is known. I hope, therefore, that the photographs reproduced in this volume will be of real value as a scientific record of the wonderful power of cryptic and deceptive coloration in nature. They have been obtained over a period of some fifteen years, from many parts of the world, and, unless otherwise stated, they represent wild animals, free and in their natural surroundings.

All the figures in the text I have drawn specially for the book. Figs. 8, 24(1), 28(2), 48, 50, 54, 69(2), 73, 75, 82 and 83(2, 3 and 4) are copies in line of existing half-tone illustrations whose source is named in the text. Fig. 56 is based partly upon photographs of the Crested Rat in display, kindly given me by Mr. David Seth Smith, of the Zoological Society of London. Fig. 69(1), representing the cryptic attitude of *Zabrochilus australis*, is taken from a photograph of the living insect by Mr. A. J. Nicholson, who generously supplied me both with a print and with a specimen of this remarkable grasshopper. In Fig. 74 the cryptic attitude of the Poor-me-one is taken from a photograph by A. Muir, published in the *Ibis*, 1925. The remaining figures are original.

Sir John Graham Kerr, F.R.S., M.P., has paid me the compliment of showing a lively interest in this work since it began to take shape, nearly five years ago, in the Department of Zoology, Glasgow University; and his never-failing encouragement, guidance, and friendship, backed by his own exceptional store of knowledge and experience both as a field naturalist and as an authority on questions of camouflage, have contributed much towards the confident spirit in which I have been able to approach the work. In addition to the untiring support he has given me, he has generously found time to read through and correct the

entire proofs. To Dr. Julian S. Huxley, D.Sc., F.R.S., I am also under very real obligations. He, too, has read the whole book in proof, and has spared no pains in giving helpful criticism. I appreciate my good fortune in having had the benefit of advice and numerous valuable suggestions from one whose own important contributions to knowledge in the field of adaptive coloration is so widely recognized.

It is not possible to mention here the names of all those who, in one way or another, have generously given advice or assistance. They know, and I appreciate, in what ways they have helped. To various officials of the British Museum (Natural History) I am indebted for facilities which they have so courteously granted, and in particular I wish to thank Mr. H. W. Parker, M.A., and Mr. J. R. Norman, of the Department of Zoology, and Mr. W. E. China, of the Department of Entomology, for giving me access to specimens in their charge, and for helpful suggestions and many kindnesses. At Oxford, Professor G. D. Hale Carpenter, M.D., has kindly allowed me to examine and photograph specimens in the Hope Department. I am also especially indebted to my friend and former travelling companion, Mr. L. C. Bushby, of the Zoological Society of London, for the opportunities he has afforded for the study of living insects in the Society's Gardens.

I owe a debt of gratitude to the Colston Research Society, Bristol University, for a grant towards expenses incurred during a zoological expedition to the Canary Islands in 1931; and to the Carnegie Trustees for the Universities of Scotland, for financial assistance received in 1937–38 during my tenure of a Carnegie Teaching Fellowship in the University of Glasgow.

To my publishers I should like to express my indebtedness for the courteous consideration they have shown me, and for the care which they have bestowed on the book in all stages of its production.

Finally, I must record a deep sense of gratitude to my wife, who has typed part of the manuscript, checked the final proofs, helped me to compile the index, and who in innumerable other ways has lightened my work.

This book was written in a period of unsettled peace, in which the nations of Europe were preparing for, or against, war. Now the war has come, and with it an intensification of industrial energy and of that preoccupation with machines which has long been an accompaniment of modern life. In these days that lie ahead, when too exclusive an interest in mechanical and scientific contrivancies must tend to encourage the development of what Lord Dawson once called the 'gadget-mind', which is restless, unreflective, and unemotional, the study of natural history provides a welcome antidote—not indeed as a way of escape from reality, but rather as a means of seeing, as from a mountain-top, and in clearer and wider perspective, that struggle for existence which is the lot of men not less than of animals.

In war, as in peace, to young and old alike, animals may be, and should be,

a fount of joy and inspiration. It was Thomas à Kempis who said: 'If indeed thy heart were right, then would every creature be to thee a mirror of life, and a book of holy doctrine.' All men, provided they are not too ignorant, too proud, or too sophisticated, are bound to take a delight in animal life; and fortunate are those who have learned to see, in the wild things of nature, something to be loved, something to be wondered at, something to be reverenced, for they will have found the key to a never-failing source of recreation and refreshment.

Unmindful of the affairs of men, the pageant of nature marches on: we can recognize and give names to most of the actors; but of their make-up, their parts, and their inner lives we still know little enough. In whatever direction we look, there appear problems, old and new, awaiting investigation. Much, then, remains to be done. For the research worker with patience, resolution, and imagination, the future is full of promise. Experimental embryologist and biochemist, physiologist and psychologist, systematist and ecologist, each views the players from a different angle; each has a special light to shed upon them; each may help to banish the dark shadows and dusty corners into which we cannot yet see clearly. I hope that with the present volume I have been successful in sending a ray or two across this old stage of nature—a stage crossed by so fine and varied a cast that those privileged for a few fleeting years to see the show may well look on in wonder, and in gratitude.

HUGH B. COTT

UNIVERSITY MUSEUM OF ZOOLOGY,
CAMBRIDGE

January, 1940

此为试读,需要完整PDF请访问: www.ertongbook.com

CONTENTS

PART I: CONCEALMENT

THE METHODS BY WHICH CONCEALMENT IS ATTAINED IN NATURE

1. GENERAL COLOUR RESEMBLANCE

2. VARIABLE COLOUR RESEMBLANCE

3. OBLITERATIVE SHADING

4. DISRUPTIVE COLORATION

5. COINCIDENT DISRUPTIVE COLORATION

6. CONCEALMENT OF THE SHADOW

THE FUNCTION OF CONCEALING COLORATION IN NATURE

7. CONCEALMENT IN DEFENCE, MAINLY AS ILLUSTRATED BY BIRDS

8. CONCEALMENT IN OFFENCE

9. OBJECTIONS AND EVIDENCE BEARING ON THE THEORY OF CONCEALING COLORATION

WARNING COLORATION IN REFERENCE TO PREDATORY ENEMIES

8. EXPERIMENTAL EVIDENCE THAT VERTEBRATE ENEMIES LEARN BY EXPERIENCE

9. EVIDENCE OF SELECTIVE FEEDING BY VERTEBRATE ENEMIES IN A STATE OF NATURE

PART III: DISGUISE

SPECIAL PROTECTIVE AND AGGRESSIVE RESEMBLANCE

1. SPECIAL RESEMBLANCE TO PARTICULAR OBJECTS

2. ADAPTIVE BEHAVIOUR IN RELATION TO SPECIAL CRYPTIC RESEMBLANCE

3. ADVENTITIOUS CONCEALING COLORATION

CONSPICUOUS LOCALIZED CHARACTERS

4. DEFLECTIVE MARKS

5. DIRECTIVE MARKS

此为试读,需要完整PDF请访问: www.ertongbook.com