CONTROLLED
NATURAL SELECTION
AND VALUE MARKING

J. C. MOTTRAM

Cornell University Library
Ithaca, New York

BOUGHT WITH THE INCOME OF THE
SAGE ENDOWMENT FUND
THE GIFT OF
HENRY W. SAGE
1891

Cornell University Library
QH 366.M92

Controlled natural selection and value m

3 1924 003 050 428

mann

Cornell University Library

The original of this book is in
the Cornell University Library.

There are no known copyright restrictions in
the United States on the use of the text.

**CONTROLLED NATURAL SELECTION
AND VALUE MARKING**

CONTROLLED NATURAL SELECTION AND VALUE MARKING

BY

J. C. MOTTRAM, M.B. LDN.

LONGMANS, GREEN AND CO.
39 PATERNOSTER ROW, LONDON
NEW YORK, BOMBAY, AND CALCUTTA

1914

All rights reserved

PREFACE AND INTRODUCTION

THIS small volume makes public a new Theory. At the outset it is most important to make clear that no attempt is made to prove the Theory. For this reason it would have been better perhaps to have called it a New Hypothesis. Nevertheless, although proof is not attempted, the numerous examples mentioned for purposes of illustration are, in themselves, facts which the Theory correlates, and therefore to some extent put the Theory to test.

One reason why proof is not attempted, is that many and important observations which would best test the Theory, have either not been made or records of them have not been found. So much is this the case, that one of the chief reasons in bringing forward the Theory is to stimulate such research. Another reason is that it supports Charles Darwin's Causo-mechanical Theory of the Origin of Species. A weak part in this great Theory is and always has been the subsidiary

Theory of Sexual Selection. If therefore it could be shown that the origin of secondary sexual characters does not require this second Theory for their explanation, and if at the same time it can be shown that the origin of these characters is precisely similar to that of all characters: then the greater Theory, instead of being weakened by the Theory of Sexual Selection, will be strengthened by this widening of its capacity. This is the endeavour of the new Theory.

It follows, therefore, that it has as a foundation—Darwin's Theory of the Origin of Species, and thus it has support: but it is also open to all the many arguments which are levelled against this foundation. The Theory does not deal only with secondary sexual characters, but also with very many others which cause di- or poly-morphisms. The Theory is described as much as possible in simple language; technical words are whenever possible avoided, in order that it may be intelligible to naturalists and field observers, for it is their valuable work which is required for its substantiation or the reverse. New terminologies are not introduced, although for descriptive purposes they would have been invaluable, because on account of

the hypothetical nature of the thesis, they did not appear to be justified. Repetition has been avoided as much as possible, even at the expense of forward reference, so that the whole volume must be read in order that a clear understanding may be obtained. The volume is divided in the following manner: Chapter I states the Theory; Chapters II, III, and IV deal at length with some facts on which the Theory rests; the remaining chapters exemplify the Theory.

Exception will probably be taken to some of the premises chosen, to some of the steps in the arguments; but entrance into this most difficult subject is made only with great diffidence. Nevertheless hope is entertained that even if the Theory does not correlate a good number of the facts to which it is applied, it will at least explain a few. Even if it does no more than lead other minds along new lines of thought, the author will not be dissatisfied.

CONTENTS

CHAP.	PAGE
PREFACE AND INTRODUCTION . . .	v
I. THE THEORY	1
II. CONSPICUOUSNESS IN NATURE	12
III. CONSPICUOUS COLOUR	21
IV. THE SELECTING POWER OF ENEMIES	42
V. FAMILY INSTINCTS	62
VI. THE COPULATORY ATTITUDES OF THE PAIR	67
VII. PRE-COPULATORY DISPLAYS	73
VIII. SEXUAL COLOUR	78
IX. PARENTAL COLOUR	91
X. PARENTAL AND SEXUAL CHARACTERS	98
XI. CONSIDERATION OF BRITISH BIRDS	107
XII. HUMAN AND OTHER SOCIETIES	122

CONTROLLED NATURAL SELECTION AND VALUE MARKING

CHAPTER I

THE THEORY

BEFORE statement of the Theory is given, certain facts of Nature must be called attention to, upon which the Theory may be said to rest.

Firstly, the individuals of a species are, in very many cases, not all of equal value. In the vast majority of sexually differentiated species, males are less valuable than females, for these reasons:—the soma carrying the female germ cells, the female, does not discharge its germ cells until they are fertilised, and often partially developed into embryos. Thus the female often is equivalent to male and female, and when about to give birth to young, to male and female in the form of young, individuals of the next generation.

2 CONTROLLED NATURAL SELECTION

On the other hand, the soma carrying the male germ cells, the male, discharges its germ cells before fertilisation, and therefore is at no time bisexual, as the female can be. For another reason, males are less valuable than females—because the male can fertilise a *number* of females; therefore fewer males than females are required by a species. Further, as the sexes at birth commonly are approximately equal, and the environment of a species is always limited, and a species is best off when it fills its environment with individuals capable of the greatest fertility . . . it follows that males, when in excess of females, or when equalling them in number, or perhaps even when somewhat less numerous, must be less valuable than females. Besides a difference in the value of individuals according to sex, there is a difference according to age.

A very old and sterile, or relatively sterile, individual is not only valueless but harmful to the species, in that it fills a place that a fertile individual should occupy. Young are more valuable than old, because they have a longer life for reproduction before them.

There are other factors which give individuals of a species differences in value,

but sex and age are by far the most important.

The next fact that attention is drawn to, is that within a species individuals often differ widely in structure and characters. Males differ from females, young from old, in form, colour, structure, habits, instincts, and in many other characters apart from their sexual organs.

These differences within a species are apparently often greater than the differences which distinguish one species from another (compare male and female pheasant with House and Tree sparrows), and are infinitely greater than the variations always to be found in every species, and by means of which, according to Darwin's theory of the Origin of Species, evolution has taken place.

Attention to one other fact must be called, —namely, that individuals of a species often form themselves into societies: males and females become mated and form pairs, which keep together throughout the breeding season, or it may be for life. Parents and young also often keep together, forming families; or families may meet to form herds; societies which may be temporary or permanent. More complicated societies are not unknown; for instance, the hive bees.

4 CONTROLLED NATURAL SELECTION

On these three facts the theory may be said to rest :

1. Within a species, individuals differ in value.

2. Within a species, individuals differ in structure.

3. Within a species, individuals form societies.

Further, there is a correlation between these facts, in that the differences in value are associated with the differences in structure. Females are more valuable than males ; females differ in structure from males other than in their sexual organs. Young are more valuable than old, and they too are different in structure. The third fact is also correlated, in that difference in structure between male and female and between young and old are especially to be found in those animals which are closely united socially, either sexually or into families.

The theory can now be stated under four headings :

1. Natural Selection appreciates the differences in character which distinguish male from female, young from old.

2. Natural Selection must treat associations of individuals as units, just as it does single individuals.

3. Natural Selection, just as it brings about diversity of structure by acting on individuals, so it must bring about diversity of structure by acting upon associations of individuals.

4. These diversities of structure found in the unequally valuable members of societies, control Natural Selection in such a way that the less valuable are more liable to destruction than the more valuable.

1. If Darwin's theory of Natural Selection accounts for the evolution of organic matter, if Natural Selection appreciates the more or less small, continuous, or discontinuous variations which occur among the individuals of a species, or even if it cannot appreciate these but only larger variations, mutations — if Natural Selection can do this, it must appreciate the relatively great differences which frequently distinguish male from female, old from young. If the scales of Natural Selection can detect a small difference between two individuals, it must be able to easily detect great differences.

If chance alone does not govern the selection of very similar individuals, it is unlikely to do so when the individuals are very different. If the chance of taking one bird out of two hen birds is not half, because,

6 CONTROLLED NATURAL SELECTION

although apparently similar, they are in fact not so ; then the chance of selecting one out of male and female birds must also not be half ; and in this case, because the individuals are markedly different in structure, it is likely to be further removed from half than in the case of the apparently similar hens.

Thus these great differences in structure between male and female, young and old, *must* cause the male and the old to be *more or less* liable to be selected than the female and the young. One cannot conceive these individuals having an equal chance of survival in the struggle for existence.

Continuing this conception further, a question at once arises : May not these differences in structure between male and female, young and old, be such, that the more valuable females and young may have a better chance of survival than the less valuable males and old ? may not this be their purpose ? This question, although asked now, is answered under heading 4, and is best answered after headings 2 and 3 have been discussed.

2. Natural Selection must treat associations of individuals as units, just as it does individuals. If, within a species, owing to the struggle for existence, the fittest individuals

alone survive—if the law of the survival of the fittest be true—then this law must also apply to pairs, families, or other societies of individuals, either temporary or permanent.

If a pair A is better able to fit the environment of the species than pair B, then pair A will have a better chance of survival, and so of reproducing themselves, than pair B. The male of pair A may not be better than the male of pair B, or the female of pair A than the female of pair B; it is the combination that matters and not the individuals.

So with all societies. If a community of bees A possess, as a variation, a character which enables them to better resist their enemies than a community B not possessing this variation, then community A will survive and reproduce, whilst B will succumb. In fact, directly individuals form themselves into societies, whatever be the bond, whether close or very slight, then they at once cease to be units *re* natural selection, *re* the survival of the fittest; the society, the pair or the family at once becomes the unit. Males may be perhaps compared with males, females with females—this male may be said to be fitter than that; but as long as the association lasts, an individual's mate is as much a part

8 CONTROLLED NATURAL SELECTION

of himself, as any of his personal characters, *re* evolution.

Those structures or characters of the individuals forming the society, which are alike, being common to all, can of course be considered as units if desirable; but those structures or characters peculiar to, say, the male of a pair or of a family, cannot and must not be considered apart from the pair or the family.

This conception has been carried thus far, in order that the explanation of heading 3 may be more easily understood.

3. *Natural Selection, &c.*—If the fixation of a useful variation in an individual is brought about by heredity and Natural Selection, then when a useful variation occurs in a society, although it may be confined to only one class of individuals and not be found in all the classes of individuals forming the society, it none the less will become fixed in a like manner.

For instance, certain males of a species may develop, as a variation, a certain character which, although not beneficial to them, or it may even be harmful to them, is, however, useful to the pair, male and female; enabling the pair to survive in the struggle for exist-

ence, and to reproduce itself, better than other pairs whose males do not possess this added character. Such a character, associated in the first place with maleness, will be handed down by the male to the pair's male offspring. Such a character should be looked upon as a character of the pair and not of the male, although bound to him.

So with other societies, parents or young may possess, as variations, characters which enable the family to reproduce itself better than other families. When these become fixed they must be looked upon, not as characters of old individuals or young, but as family characters.

It is possible to now explain heading 4.

4. *These Diversities, &c.*—If pairs, families, or other societies have characters, and if, within these societies, there are individuals of different value, then these societies must possess characters which compel Natural Selection to select the less valuable individuals rather than the more valuable.

Suppose a pair be subjected to selection, and suppose the male has, as variations, a character which causes the selecting agent to destroy him, the less valuable, rather than the female, the more valuable ; then this pair will

10 CONTROLLED NATURAL SELECTION

have an advantage over other pairs, in which the chance of male and female surviving is equal.

If the female be destroyed, the character of the female and the male will not be reproduced; at any rate the chance of his, the male, reproducing himself is less than males in general, for he must find another mate.

If the male be destroyed, it by no means follows that the male characters will be destroyed, for it is likely that he has already fertilised the female, especially as the society, a pair in the majority of animals, only occurs during the breeding season.

Directly the percentage of males in the population become much reduced polygamy results, and the value of the male will rise until it equals that of the female: directly this balance is struck, further evolution of the male, making him more liable to be selected, will cease. Similarly with any other society of unequally valuable individuals, they will become marked according to their value, and in such a way that Natural Selection will be controlled and compelled to take the less valuable rather than the more valuable.

A review of the exposition. Facts :

1. Individuals of a species not of equal value : male and female, old and young.
2. Individuals form themselves into societies : pairs, families, herds, &c.

3. Individuals differ widely in structure : male from female, young from old.

4. Correlation of these three facts : unequal value with difference of structure, and both with the formation of societies.

Sequence of argument :

1. Natural Selection must appreciate differences in structure ;

2. Natural Selection must treat associations as units ;

3. And bring about diversity of structure in them ;

4. Which structures control Natural Selection, so that less valuable individuals are more liable to be destroyed than more valuable.

Thus when male is found to be different from female it is necessary to inquire whether the difference be due to (1) a character of the individual which fits a monosexual environment, or (2) a character of the pair, also of cause an environmental character, that *controls* Natural Selection. And so with all structures occurring in sociable animals and confined to particular individuals.

Thus it is as a working hypothesis that this new theory is brought forward, in the hope that it may possibly explain the origin and use of some polymorphisms.

CHAPTER II

CONSPICUOUSNESS IN NATURE

BEFORE proceeding to exemplify the Theory, it is necessary, as will appear later, to consider the methods by which animals render themselves purposely conspicuous. Many ways are utilised ; they may be conveniently described under the following headings: Movement, Form, Position, Colour, Sound, Scent.

Conspicuous Movement.—It is freely admitted that, in Nature, moving animals are more conspicuous than resting ones ; the more perfect the rest, the less conspicuous is the animal. The simulation of death by the suspension of every movement is commonly employed by animals for protection, and examples are to be found among every class of animals.

The majority, the vast majority of animals, must perform various movements for the obtaining of food, for reproduction and other vital processes. These motions are necessary,

in spite of the fact that animals thus render themselves conspicuous to their enemies. Means are usually taken to make them as little conspicuous as possible ; they are carried out under cover, or at night, or only after inspection has proved the absence of any enemy. At the slightest alarm they cease.

It is not to this kind of motion that attention is now to be drawn, but to those motions made by animals whose purpose is to make themselves conspicuous. Motions of this kind, purposely conspicuous, are made chiefly for two reasons : (1) to signal to friends ; (2) to signal to enemies. Signals to friends give notice of danger, of security, of the presence of a comrade, of the presence of a male or female, and of many other things.

It is not to these signals, but to the signals to enemies, that attention is now directed. Signals to enemies are of two kinds, and made for two reasons : (1) *Repellent*, to repel the enemy, to frighten it away ; (2) *Attractive*, to attract the enemy, to draw its attack. Examples of these two kinds of signals by motion are to be found widely distributed throughout the animal kingdom. The majority of animals at bay attempt to frighten away an

14 CONTROLLED NATURAL SELECTION

enemy by making some menacing movement ; even quite small animals, insects for instance, will then make threatening motions. Under Repellent motions would also be classed Warning motions ; those which presuppose knowledge on the part of the enemy, the attacker ; a knowledge gained by previous association of the motion with some unpleasantness. There is considerable evidence that this kind of motion is frequently mimicked.

These signals by movement are, as a rule, associated with numerous other displays—displays of position, attitude, colour, sound, and scent ; for this reason they are difficult to analyse. It is often difficult to decide whether the motion is the essential or an accessory of the signal.

(2) *Attractive*.—Motion signals, whose purpose is to attract an enemy, although frequently overlooked, are also common in Nature. Amongst birds, as mentioned in Chapters V and X under Family Instincts, parents will frequently endeavour, by the making of conspicuous movements, to attract an enemy, to draw its attack. Numerous other examples will be given when consideration is made of Sexual Displays. Purposely conspicuous movement is probably, therefore,

an entity in Nature, and may be conveniently classified thus :

Purposely conspicuous movements.	1. Signals to friends.	
	2. Signals to enemies.	<div style="display: inline-block; vertical-align: middle;"> <p>(a) Repelling conspicuous movement: to repel an enemy, to frighten it away.</p> <p>(b) Attracting conspicuous movement: to attract an enemy, to draw its attack.</p> </div>

Position.—Conspicuousness as the result of position cannot properly be considered apart from the animal's surroundings, their form and colour. A moth resting on a tree-trunk may be conspicuous or not, according as its form and colour contrasts or harmonises with that of the tree. However, there is little doubt that some animals sometimes, and others frequently, purposely take up positions which render them conspicuous in Nature. It is not always easy to decide whether any given observed position of an animal which is conspicuous is the result of accident or purpose. Only by a thorough knowledge of the habits of the animal, and after many observations have been made, can this be decided. For in every animal's surroundings can be found that which will render it, on the one hand, conspicuous, or

16 CONTROLLED NATURAL SELECTION

on the other, inconspicuous. The form, colour, and habits of the animal may be such that it is seldom or never found among surroundings which render it inconspicuous; or its form, colour, and habits may produce the opposite effect; unfortunately our knowledge of the habits of animals is so small (possibly because our attention has been chiefly concentrated on the study of their other characters) that we are usually unable to decide whether the observed position in Nature of an animal is conspicuous or inconspicuous, the result of accident or purpose.

Further analysis of this method will not be gone into, especially as it must again be frequently referred to when dealing with other methods.

Form.—By form, animals can be and are more readily recognised than by any other attribute; in fact, it is by the amount of space they occupy that we know them. There are, no doubt, species which are more easily distinguished from closely allied species by colour or some other character, because they are alike in form and size; but the mind, unconsciously, first places them according to their form.

A wasp is recognised, first by its shape,

but afterwards the mind may decide what species of wasp it is by its colour, or some other character. For this reason, *form per se* is a character which the majority of animals endeavour to hide, because the majority of animals wish to make themselves inconspicuous in Nature. So much is this so, that a study of protection is in truth a study of the means used to obliterate form. Nevertheless, some animals which are purposely conspicuous in Nature take no precautions to obliterate form, but, in fact, rather accentuate their shape; these may be said to possess purposely conspicuous form.

Thayer has shown that form is commonly rendered inconspicuous by oblitative shading.

Absence of oblitative shading or anti-oblitative shading, when found in animals whose form could be concealed by oblitative shading, will be examples of purposely conspicuous form.

Purposely conspicuous form may be classified like purposely conspicuous motion, according as the signal is to friends or to enemies.

Mention has already been made of conspicuousness, produced by the taking up of particular positions; this may be accentuated by the assumption of some easily seen form in

18 CONTROLLED NATURAL SELECTION

that position. Animals in defence, in order to beat off an enemy, will erect combs, feathers, or hairs, will open mouths, stretch necks, take up an upright position, and in many other ways assume conspicuous attitudes; these may be called Repelling Conspicuous Attitudes. Just as there are attracting conspicuous movements, so there are attracting conspicuous attitudes. Many animals by thus making themselves conspicuous endeavour to draw an enemy's attack, for instance, from their young. Birds especially will erect combs, spread tails, and assume all manner of conspicuous attitudes for this purpose. A large number of pre-copulatory displays consist in the assumption of conspicuous attitudes.

Sound.—Sound is seldom used for ought but signalling to friend or foe. Silence spells concealment, sound conspicuousness.

Sound can be similarly classified :

Purposely conspicuous sounds.	1. Signals to friends.	(a) Between the sexes.
		(b) Between members of other societies.
	2. Signals to enemies.	(a.) Repellent (conspicuous) sounds: to frighten an enemy away.
		(b) Attractive (conspicuous) sounds: to attract an enemy, to draw its attack.

Repellent sounds are very commonly used to ward off a foe: sudden and therefore startling sounds are especially used. Attracting sounds, to draw an enemy's attack from the young, are often difficult to distinguish from the alarm notes made to warn the young of danger; it may be that sometimes the same note is used for the two purposes. The cry of the Plover or Curlew certainly causes the young to take cover, and more than likely distracts the enemy's attention from the young to the screaming parents.

Evidence will be brought forward later to show that the songs of birds are to protect the female, by drawing the attention of any near predatory animal to the singer, the male.

It may be here mentioned that the drawing of an enemy's attack is not in any way an act of self-destruction. Predatory animals usually take their victims by surprise, and probably then stand as good a chance of making a successful capture, as when the victim is purposely exposing itself in order to draw attack.

Scent.—Scent is used precisely like Sound. Repellent scents are always unpleasant; but owing to the inferiority of our sense of smell,

knowledge of the subject is meagre, and probably untrustworthy. It may be that there are pleasing scents, the purpose of which is to attract enemies.

One other method, by means of which animals render themselves conspicuous, remains to be considered, namely colour. This has been left to the last, because it is the most important and because a previous consideration of the other methods may render its consideration more comprehensible. This is dealt with in the next chapter.

CHAPTER III

CONSPICUOUS COLOUR

It is not possible to conceive that the colour of an animal, in Nature, is purposeless, indifferent, the result of chance. The colour of domesticated animals may be conceived to be of such a nature, but if one believes in the Origin of Species as expounded by Charles Darwin, then the colour of animals in Nature must be looked upon as purposeful; and it can have but two uses: (1) to make an animal inconspicuous, (2) to make it conspicuous. This it can only do by contrast; to consider the colour of an animal *per se* must be meaningless; only the comparison of its colour with that of its surroundings can be of any value. Therefore when considering the colour of animals, at least three factors must be taken into account: (1) the colour of the animal, (2) the colour of its environments, and (3) the animal's habits. Without a knowledge of its habits, it is impossible to decide whether an

22 CONTROLLED NATURAL SELECTION

animal is conspicuous or inconspicuous in Nature, wherein all kinds of backgrounds are to be found, backgrounds which will render the most brilliantly coloured animal inconspicuous, and backgrounds which will make the dullest easy to see. For this reason, the animal's habits must be taken into account ; it is necessary to know whether a given animal is commonly or uncommonly seen against obliterating backgrounds. It is also necessary to know, for instance, in the case of butterflies, what are the common backgrounds found behind the insects on the one hand when they have open wings, and on the other, when they have closed.

Colour rarely is used for other purposes. Metabolic processes may give rise to colours which are purposeless, apart from metabolism. Waste products which have to be got rid of, may be deposited on the surfaces of plants and animals.

Colour may have other uses ; for instance, black for the absorption of the sun's heat, white for its reflection : the green chlorophyl of plants comes under this category.

Reference will again be made to Habits, when Thayer's theory (that all animals are protectively coloured) is being criticised ; in the meantime, apart from habits, certain generalisations of colour in Nature can be made.

The face of our earth is, broadly speaking, coloured with secondary colours, greens, browns, and greys; these colours are not laid down in flat tints but in broken masses, which run one into the other, and nowhere have defined margins. Individual leaves and single stones can only be distinguished at close range, and are then seen never to be homogeneously coloured.

Certain portions of the globe are not so coloured. The Arctic regions, mountain tops, and sub-arctic regions in the winter are covered with an even cloak of white; deserts are evenly coloured light brown; oceans grey or blue; sky blue.

Into these backgrounds many animals fade, through similarity of colouring. Spotted coats and barred plumes of brown, green, and grey blend with the field and forest; white animals in the snow, sandy-coloured in the desert, grey at sea, &c., are invisible from afar.

Against these backgrounds certain parts of plants and many animals stand out in marked contrast—how are they coloured? In an exactly opposite manner: instead of being coloured with secondary colours, the primary ones are used, red, yellow, blue, with black and white; and instead of the colour

being laid down in broken masses, it is painted on in broad flat tints. In this way the maximum contrast is obtained. Flowers are purposely conspicuous, so that insects and birds may see and visit them; they are coloured with even washes of the primary colours and with white. White daisies, yellow buttercups, blue cornflowers, red poppies, are examples always to hand; green, grey, or brown flowers form a very small percentage of the whole; they as a rule do not desire the visits of the hoipolloi of insects, but of one particular insect which they attract by scent or some other method, apart from colour.

The efficiency of this method of making themselves conspicuous in Nature is patent to everyone who views wild flowers; they will not be passed by unseen; on the other hand, brown and green flowers require diligent searching for, with a well-trained eye. The same may be said of edible fruits which present purposely conspicuous colouring; they are found to be coloured with the primary colours and with black and white, laid down evenly.

Turn now to animals. Many are undoubtedly protectively coloured with mottled greens,

greys, and browns ; but there are others which are painted with broad masses of the primary colours and with black and white. May not these present, like fruit and flowers, seeing that the same method is used, purposeful conspicuous colouring ?

A more detailed analysis of these colours will now be made.

White.—In regions where snow, either temporarily or permanently, covers the ground, white is used cryptically or protectively. It is used also on the under-sides of many animals, to produce oblitative modelling, as Thayer has shown. Thayer is of opinion, too, that it may also be used to conceal an animal against the sky ; but when a flat white surface is held against the sky at different angles, it will either appear much darker than, or if the sun is out, much lighter than the white of the sky and be very conspicuous ; only within a very small angle will it be equal in tone to the sky. Further, only a very small portion of the sky can be thus matched, away from the sun and not far above the horizon. Thus it appears that only with care, and in one particular position, can a FLAT white surface be made to appear inconspicuous against the sky : with a solid white object,

it is of course quite impossible. A swan, for instance, must always be conspicuous against the sky. White, therefore, except in snow and to produce oblitative modelling, will render an animal conspicuous in Nature.

Black.—As with white, it is possible to conceive of a black animal being invisible, for instance, against a black shadow : a rook sitting in the innermost recess of a thick forest would be difficult to see ; but black shadows are almost unknown in Nature, especially cold black, such as is found in many animals. Shadows in Nature are invariably warm, because the objects in them are lit by the reflected light from surrounding warmly coloured objects.

Animals coloured black, and especially cold black, must therefore be looked upon as conspicuously coloured. Attention had again better be called to the fact, that it is not enough to study colour alone ; habits must also be taken into account. A black animal, living in dark forests and always shunning the light, cannot be compared in conspicuousness with a black animal which lives in open country, *e.g.* the female Blackbird with the Starling or Rook.

Black therefore must be looked upon as

conspicuous, unless contradicted by the habits of the animal.

Blue.—Blue, in Nature, is found in the sky and in its reflection in water and snow. If white animals are seldom, if ever, inconspicuous against the white (light grey) of the sky, then blue animals can never be in harmony with the blue of the sky. The amount of blue light coming from a blue sky is enormous compared to the amount coming from an object coloured even very light blue, and placed in the brightest sunlight.

It is therefore impossible for a terrestrial animal coloured blue (a blue butterfly for instance) ever to be in harmony with a blue sky. Blue, used protectively, is however found in oceanic fishes inhabiting the surface of the water; as a rule their dorsal surfaces are coloured blue, in harmony with the low-toned blue of very deep water as it is seen from above. Now the blue of these fish is not less brilliant than the blue found in terrestrial animals; and as this blue harmonises with the low-toned blue of the sea, it cannot, in terrestrial animals, ever harmonise with the intensely high-toned blue of the sky. It thus appears that the blue of terrestrial animals is not protective; and if not protective, it must

be purposely conspicuous, as it cannot be indifferent.

Yellow.—The primary colour, yellow, is a very rare environment for animals, and so it is very rarely used protectively. A few insects which fly in the autumn are yellow, in harmony with the yellow autumnal foliage. Sunlight penetrating young green foliage is not a pure colour but yellow-green ; this colour is found on the breasts of a number of birds, the Willow Wren (*Phylloscopus trochilus*) for instance ; compare this with the yellow bar in the Goldfinch's (*Carduelis elegans*) wing, and with the yellow of the male Golden Oriole.

Red.—Above all others, animals coloured red are the most conspicuous in Nature, because it is never found in the surroundings. The rising and setting sun sometimes colours all things red, animals as well as their surroundings. Thayer is of opinion that some scarlet animals, Flamingoes (*Phœnicopterus ruber*) for instance, are coloured thus to render them invisible against the red of the setting sun ; that which has already been said about sky protections, under White and Blue, also applies to Red ; a red animal against the setting sun, by contrast, looks not red but black.

Having analysed to some extent colour in Nature, and shown that some colours cannot, and others probably do not, render an animal inconspicuous, and must therefore make it conspicuous, it now becomes necessary to consider the colour and habits of animals conjointly. By means of examples it will be shown that the colour and habits of animals are correlated ; and that conspicuous colouring in animals is a fact of Nature.

The Sheldrake (Tadorna cornuta) will be the first example : the sexes are nearly similar, coloured with large masses of black, white, and red ; it lives in estuaries, on mud flats and sand banks, it nests in sand hills ; among these surroundings, no matter at what angle it is viewed, it is an object visible from afar, often at a distance of several miles. It is possible to conceive of a background, of boulders for instance, or of different coloured seaweeds on white sand, against which the bird would not be conspicuous : just as it is easy to conceive of a background against which it would be conspicuous : but ask the wild-fowler or longshoreman which is the most conspicuous bird on the shore, and he will say—the Sheldrake. Systematically watch the birds over a long period of time

and from different heights, from the tops of cliffs as well as from the bases, not once in a day will they become difficult to see.

If the Sheldrake is protectively coloured, and this is the only alternative, then why does it utilise a different colouring from the other shore birds, which are undoubtedly protectively coloured—the Waders, &c.? If, on the other hand, it is conspicuously coloured, how does it manage to hold its own against hawks and other predatory animals? By living always in open country where it cannot be approached unawares, by always being close to water where it can seek safety by diving.

Why is it conspicuously coloured?

Although to show the *raison d'être* of conspicuous colouring would add much to the above argument, this must be reserved for a future chapter, in order to prevent confusion and overlapping of the subject.

The next example chosen is the *Stonechat* (*Pratincola Rubicola*), a bird presenting a very similar colour to the Sheldrake—black, red, and white. These are its habits. It lives and breeds on open commons, always a conspicuous bird from its habit of constantly perching on the topmost branches of the

furze bushes. Stonechats have been observed for many hours at a stretch and from all angles, but only on very rare occasions are they difficult to see, as when they have dropped down for a moment on to broken ground after some insect food. They never depart far from their undergrowth of furze or briar, so have constantly at hand a secure refuge in case of attack, and thus do not require protective coloration. The usual background of this bird is the sky and dark bushes, not broken ground.

Consider the *Rook* (*C. Frugilegus*). In the early morning the flock leave the woods, to spend the whole day in the open country, where they are a mark for miles around, especially on a day of sun, for then the flashes of light from their glossy plumages will reveal their presence three or four miles away. In a tree the bird is equally visible as a dark mass against the sky. When it is possible to look down on a colony of their nests, the sitting birds stand out blue-black in marked contrast to the broken brown of the nests. The Rook is a social bird: there is safety in numbers: it will be an advantage to a single lost bird to be able to see the flock from afar.

The Soldier Beetle (Telephorus) is conspicuous in Nature, not entirely because it is coloured black and red, but because it chooses to spend its days on the surfaces of white umbelliferous flowers, whence it can be seen from afar and is at the mercy of any bird who cares to feed upon it.

The Black Beetle (Pimarcha lævigata) is coloured an intense, cold, blue-black. It is a beetle which is at large during the day, crawling sluggishly and clumsily about and taking no pains to conceal itself: a very conspicuous object. If given to birds, they will either not take them, or having picked at them will spend many minutes scraping their beaks, obviously in an endeavour to get rid of a very unpleasant flavour; they will seldom swallow these beetles. The Soldier Beetle is similarly treated.

The Cinnabar Moth (Euchelia Jacobææ). Coloured black and vivid red: it flies by day: it is a slow flier and would fall an easy victim to any enemy: it never takes any pains to conceal itself, as other insects do when disturbed: it does not bury itself in the grasses: it does not seek safety in flight.

The Large White Butterfly (P. brassicæ). A slow flier—it can be seen at least 500 yards

away—it would fall an easy victim to any bird. In London, where the Sparrows have had little experience of White Butterflies, I have on several occasions (four) seen Sparrows (*P. domesticus*) take them on the wing, but always, after pecking them and killing them, they have left them. Apparently they are relatively unpalatable.

The Red Admiral Butterfly (*Pyrameis Atalanta*) spends many hours of the day, with outstretched wings, on flowers: flat flowers are especially chosen; here it is always a conspicuous object, no matter how viewed. It depends for its safety on quickness of sight and rapidity of flight. When sleeping, it closes its wings, displaying the under surfaces only, which are not conspicuously coloured; and it chooses to rest among surroundings which render it inconspicuous—among dead leaves or on the barks of trees, &c. If disturbed whilst thus resting, it does not fly away, but relies for escape entirely on its protective colouring, and the simulation of an inanimate object.

These habits associated in the same insect, with exposure of the bright upper surfaces of the wings on the one hand, and with the dull under surfaces on the other, indicate,

without doubt, that the upper surfaces are conspicuous in Nature and the under ones inconspicuous.

It is probably an advantage for Admiral butterflies to be able to see other Admiral butterflies on flowers, from a distance ; and thus to find good food and mates, &c.

The Tadpole (Rana Temporaria), when very young, is coloured uniformly black. At this stage, they keep together in colonies, forming black wriggling masses, as noticeable from under water as from above, and make, when disturbed, no effort at concealment.

It is noteworthy that the black of the young tadpole, like the black of the frog's ovum, may be for the purpose of absorbing the sun's heat.

Experiments have shown that young tadpoles are unpalatable to both birds and fish ; it seems, therefore, that they can with safety render themselves conspicuous, and utilise the beneficial heat-absorbing property of blackness.

Sufficient examples, and they could be multiplied almost indefinitely, have now been given, to show that many animals are conspicuous in Nature and make no attempt to conceal themselves.

It appears, therefore, that Thayer's theory, that all animals are protectively coloured, does not correctly describe the facts. An artist's eye will note, or his hand be able to depict, the most brilliant animals among surroundings which render them inconspicuous; but if the animals are rarely found among these surroundings, then such observations and such illustrations appertain to exceptions and not to the rule, and thereby hide the truth.

Certain broad conclusions may now be made :

1. Animals which are coloured with the primary colours and with black and white, and on which these colours are laid down in large and distinct areas, MAY or may NOT present conspicuous colouring : a close study of their habits and surroundings can alone decide how they must be classed.

2. Animals which are coloured with the secondary colours, or with the primary colours much broken into small masses, one into the other, are almost invariably protectively coloured. But in these also, habits must be taken into account. One is now in a position to classify colour; as before mentioned, it must first be divided into Purposely Conspicuous and Purposely Inconspicuous. These

36 CONTROLLED NATURAL SELECTION

may be again sub-divided as in the following table :

COLOUR	inconspicuous	to enemies	protective = procryptic.
		to food	aggressive = anticryptic.
		(to friends)	(? valueless.)
	conspicuous	to signal to enemies	to attract enemies = attracting colour.
			to repel enemies = Aposematic. = Pseudo-semantic.
		to signal to friends	Recognition marks = Episematic.
		to signal to food	to attract food (as in Mantidæ) = Pseudo-episematic. = alluring colour.

The colour of an animal can, however, never be considered as a unit. Some of the coloured parts will be used for one purpose, others for another. For instance, in many animals and especially in birds, parts are conspicuously coloured which are usually concealed, and which are only displayed on definite occasions and for definite purposes : thus, too, the Red Admiral butterfly can, at will, display

the upper surface of its wings, or the under ones. No general statement, therefore, can be made of its coloration, but its upper and under surfaces must be separately labelled. Further, it is readily conceived that additional knowledge of its habits might necessitate qualifications of these labellings : for instance, the black might prove to be a signal to enemies, and the red bar a social signal.

Here, however, colour must be considered only in so far as it is purposely conspicuous, and especially with regard to signals to enemies.

Signals to enemies are of two kinds only : (*a*) in order to repel enemies ; (*b*) in order to attract enemies.

Examples of repelling conspicuous colouring (conspicuous colouring associated with unpalatableness) are afforded by animals which have warning coloration : it is unnecessary to give examples, but it may be mentioned that, in the opinion of many, protection is not obtained, in the vast majority of these cases, by an association in the minds of predatory animals, of unpleasantness with a particular species ; but with a particular class of animals, coloured similarly.

For instance, a bird will pass by a black beetle, not because it has tasted that particular

species, but because it is coloured black like another species, whose flavour it has sampled ; indeed the first beetle may in reality be palatable. Thus have been accounted for many cases of mimicry, and their origin, by fortuitous variations of palatable insects resembling unpalatable.

To describe a colour as a warning colour, is to describe it from the point of view of an enemy; it is a description of purpose rather than of effect. The following table, given in Professor Poulton's book, is a classification of colour for the most part from this point of view. Attracting colour has not been introduced: it would fall under *B* after some modification. The terminologies here used have been placed in their appropriate places in the table given on p. 36.

A. Apatetic Colours = colours resembling some part of environment.

- (1) Cryptic (a) procryptic = protective resemblance.
(b) anticryptic = aggressive resemblance.
- (2) Pseudo-semantic = false signalling.
(a) pseudo-semantic = protective mimicry.
(b) pseudo-episematic = aggressive mimicry or alluring.

B. Sematic Colours = signalling colours.

- (1) Aposematic = warning.
(2) Episematic = recognition marks.
[(3) ? = attracting colour.]

Returning to Table I, Repelling Conspicuous Colouring is also exemplified by Alarming Coloration; many birds will frighten away an enemy by suddenly displaying vivid colour—the distention of scarlet bladders, or erection of bright plumes. Insects also utilise this method of scaring enemies; organs coloured with the primary colours are suddenly disclosed or protruded.

Attracting Conspicuous Colouring, it will be shown, is possibly much commoner in Nature than is generally supposed; accepted examples are as yet uncommon. The bright underwings of many insects are supposed to be of this nature, that predatory animals may seize them, rather than more vulnerable parts.

Parent birds, when protecting their young, will display their brightest plumes, in order to attract the enemy's attention, to draw its attack; and many examples are given in Chapter VIII.

In the meantime, mention may be made of certain colour marks, here called attraction marks.

The eye-spots found in insects are considered to be for the purpose of attracting an enemy's attention to them in order that

it may be induced to strike them rather than more vulnerable parts, which have not eye-spots. Other marks and colourings serve the same purpose ; for instance, the brilliant under-wings of many moths.

Here are examples of purposely conspicuous characters whose function is to attract enemies. Whenever conspicuous colouring is found on invulnerable parts, the question must be asked, Is this an attracting mark ? There is some evidence that these marks are by no means uncommon. In birds, for instance, the conspicuous marks and bars on wings and tail may be of this nature. As is often the case in insects, they are concealed when at rest and displayed during flight, and may cause enemies to strike at tail or wing and thus not injure vital parts.

It is noteworthy that although young as a rule do not present conspicuous colouring, they do usually have these attraction marks. (For examples see Chapter IX.)

It will be well to review the conclusions which have been arrived at in the last two chapters :

1. Purposeful conspicuousness of animals is a fact of Nature.
2. It is produced in animals by means of

movement, form, position, sound, scent, and colour ; and probably in other ways.

3. It is used for three purposes : A, to signal to friends ; B, to signal to enemies ; and C, rarely, to signal to food.

4. The signals to enemies are of two kinds : A, to repel them ; B, to attract them.

CHAPTER IV

THE SELECTING POWER OF ENEMIES

It is impossible to conceive of an environment, without also calling to mind that which is invested. A biological environment is the sum of many factors which, added together, permit of life. A study of these factors shows that they are not homogeneous, but that each of them is made up of a continuous series of diversities. Many obviously have this constitution, such as temperature, altitude above sea-level, the relation of the different points on a tree-trunk to the points of the compass. Others seem to form a discontinuity, but in these cases steps are probably not absent, only crowded together.

Just as environment cannot be conceived alone, so living matter cannot: the two are inextricably mingled. The structure of living matter is bound to its function: and function is action on environment. Without environment, living matter could not be recognised.

The Environment of a Unit of Living

Matter.—Here, a unit of living matter is used in the sense of a single individual, one of many which, collectively, form a species. If examination be made of its environment, no matter which factor be chosen for observation, it will be found to be definitely bounded, in spite of the factor not being homogeneous.

During a definite time—this must be taken into account—a plant occupies a definite quantity of space, it takes from the soil a definite quantity of mineral matter and receives a definite amount of sunlight.

A single animal wandering on a mountain-side, climbs up and down to definite heights above sea-level.

This power of being able to adapt itself to the diversities of its environment, *within limits*, is a property of all living matter.

The Environment of a Species.—If the environment of a unit is defined, then the environment of a collection of units, a species, must be definite.

In the case of sexual dimorphism and other di- and poly-morphisms, the environment of the species would be the environments of the several types of individuals added together: the defined environment of the male added to the defined environment of the female, &c. This addition is necessary because the environment of the several types of individuals is not identical, although each is defined.

44 CONTROLLED NATURAL SELECTION

Fig. 1 is a pictorial representation of this conception ; E_1 , E_2 , E_3 , &c., are the factors of the environment, shaded, to show their serial nature ; the area enclosed by dark lines is the environment of the species. Fig. 2 is a simplified illustration. The environment of

FIG. 1.

FIG. 2.

a species can be classified into common and specific. The common environment is shared with other species (many animals breathe air and drink water) ; its specific environment it occupies, solus.

If, as has been considered, structure means

environment, it is impossible to conceive of two species occupying the same environment : because one cannot conceive of two species which, being different in structure, are yet similar in function ; which is the same as having similar relations to the same environment. Different structures, different functions, different environments—here is an analogy ; but in different structures, similar functions, and the same environment—there is none.

Allied species, or a species and an established variety of it, may occupy neighbouring environments, but never the same. If allied species do not, distant species probably cannot. Thus a species must be alone in its specific environment, and never the subject of competition with other species. On account of the absence of competition and because a species increases in geometrical progression, the species must always completely fill its specific environment ; except when it has been unable to keep pace with an increase in quantity of its specific environment. A species is rare or common, according to whether its specific environment is restricted or unconfined. As will be shown later, it is not possible to conceive of a restricted common environment, and a surplus of specific environment.

The Relation of Species to Species.—The environment of one species may form that of another—beneath forest trees, tree-ferns thrive; on the stems of tree-ferns, filmy ferns find suitable homes. The cat feeds on the mouse, whose enemy the cat is. Thus, one species can, through its environment, affect that of another; but a species, *per se*, cannot affect another species because action implies something acted upon, and anything upon which a species acts is its environment. Species may occupy a common environment, but, as will be shown, in so doing, neither each other nor their specific environments are affected.

The Species and its Environment. Their Relations.—So far, the following conceptions have been arrived at. Structure equals environment. The boundaries of the specific environment of a species are defined. Each species has its own specific environment. A species completely fills its specific environment. A species can only be acted upon by physical and biological forces, through its environment.

Further consideration must now be made of the selecting agent, the Environment. It has been shown not to be homogeneous, but

that all of its factors are parts of a continuous series. Therefore the selecting power of the environment will not be homogeneous but will be arranged through the environment, in the form of a continuous series. And as the individuals that go to form a species are not identical, but differ more or less from each, it follows that these variations of a species,

FIG. 3.

whether continuous or discontinuous, will TEND to become serially arranged through the specific environment, according to the serial arrangement of the selecting power of the environment: as is shown in Fig. 3, V_1 , V_2 , V_3 — V_n perfectly fitting E_1 , E_2 , E_3 — E_n . If discontinuous there will be gaps.

In Nature, this is prevented by inter-crossing (and migration). If the species were

distributed over an unlimited space, then the environment would be differentiated; but because, in Nature, space is always limited, this environmental classification only occurs to a limited extent; when a species is distributed over a wide area, when the environmental gradient is very slight, then this establishment of varieties and sub-species may take place locally.

The above use of such words as SPACE, LOCALLY, AREA, &c. may give the impression that distribution through space is alone alluded to: these words are used with reference to the environmental gradient, whatever be the factors of its composition.

SPACE is chosen for illustration, for clearness' sake.

Varieties and sub-species may thus become established by environmental differentiation, and, it may be, evolved into distinct species. Thus, without the help of any outside force, new species may arise within the enclosure of a specific environment, as in Fig. 4. In a similar way, the environment may become sexually differentiated when the sexes are separate, as in Fig. 5. Males often differ widely in structure from females, and occupy an entirely different environment. This sexual

differentiation of the specific environment is the only possible cause of secondary sexual characters, as this volume attempts to show. Although other theories, as for instance Darwin's theory of Sexual Selection, attempt to account for these structural differences in other ways. Also, in polymorphic species, the environment becomes similarly split up.

FIG. 4.

FIG. 5.

It has been seen that the specific environment is curtailed by the limit of the ability of the species to adapt itself to the diversities of the factors which form its environment. This property is common to all living matter, and without it Life, as we know it, could not exist. If living matter could not thus accommodate itself but could only occupy a homo-

geneous environment, then living matter would assume an infinite number of different forms, corresponding to the infinite number of the diversities of its environment ; and each form would be infinitely restricted (see Fig. 3). Associated with this adaptation must be structural alteration ; function and structure are inseparable—these are acquired characters.

Nevertheless, in spite of this power of adaptation, one cannot conceive a variation of a species, whatever its nature, displacing another species from its specific environment, which it completely fills and perfectly fits ; to accomplish this, the variation would have to differ from the parent in a great number of structures, be a great mutation and would have at the same time to fit perfectly a new environment, in fact more perfectly than the former occupier, which itself is a perfect fit ; can such a correlation come about through Chance ?

Change in Environment.—Change in environment may be quantitative ; the specific environment may increase, decrease, or disappear entirely, in which case the species will become common, rare, or extinct. The change may be qualitative, and consist in the addi-

tion or subtraction of one or more factors to or from the specific environment.

The subtraction of a factor may lead to extinction of the species ; a food supply may fail. Or if the species continues to thrive, then those structures which were related to the lost factor will degenerate. Those individuals who waste the least nourishment or sustenance on a useless organ will have an advantage over others in which this organ is more developed. Degenerated organs are found in species occupying degenerated environments. Degenerate structures will be found to vary most because of the absence of the fixing power of environmental selection.

If a factor be subtracted locally, then a local degenerate variety or sub-species will be found.

The addition of a new factor to the specific environments may produce extinction. Short of extinction, an added factor will prevent a species fitting its environment perfectly ; but sooner or later, as the result of variation of the species and environmental selection, new structures will arise which will enable the species to perfectly fit the new environment. Further addition of factors will be followed by the addition of new structures ;

in this way, there will be evolution. Highly evolved species will be found in highly complex and often restricted environments ; such species will be found to vary very little. High specialisation demands great fixity of structure. The local addition of a factor will produce local evolution and the establishment of a sub-species.

Reasons have been given why one cannot conceive of a species being displaced from its specific environment by the variety of another : for similar reasons, one cannot conceive of a variation of a species being able either to occupy an environment rendered vacant by the extinction of a species, or to discover an entirely new environment. Evolution equals environmental differentiation, the better appreciation by organic matter of the diversities of its environment. The question of competition yet remains to be considered. As has already been shown, this can only occur within a common environment, and then only when the common environment is not sufficient to accommodate the two or more species which share it. Suppose (see Fig. 6) S_1 and S_2 are two species, E_1 and E_2 are their specific environments, and E_3 a common environment, where competition is

going on. Then the common environment will be a selecting agent and will select either S_1 or S_2 ; one or other must be selected, for they cannot both be alike *re* the environment. The selected one will then include the common environment in its specific environment, as in Fig. 7. If they are very similar, then different parts of the environment having slightly different selecting powers, because of its diversity, will select, some S_1 , some S_2 .

FIG. 6.

The common environment will become divided, one part joining the specific environment of S_1 ; the other part, the specific environment of S_2 , as shown in Fig. 8. In neither case will the species be in any way changed.

This competition with the common environment cannot cause the origin of a new species, but it may possibly lead to the extinction of one.

Attention must here be drawn to the difference between competition occurring within

54 CONTROLLED NATURAL SELECTION

a species, and competition between two or more species ; to the difference between intra- and inter-specific struggles.

In intra-specific struggles, because the individuals are very similar, the struggle will be prolonged : very small differences will decide

FIG. 7.

FIG. 8.

life and death. Under these conditions evolution will proceed.

In inter-specific struggles, which take place within common environments (when they become overcrowded) because the individuals are not similar in structure, the struggle will be soon over. One species is bound to be vastly more fit than the other, and will therefore quickly displace it. Can a struggle be

long protracted between individuals as different in structure as are two species? If it cannot, then such a struggle can have no effect as regards evolution, because a relatively long period of time is required both for the origin and fixation of variations.

Two caterpillars, A and B, feed upon a certain tree ; the tree becomes rare ; competition between A and B at once begins. In a few years A will displace and render B extinct, or vice versa ; because one must possess certain characters, structures, and habits which give it a very decided advantage in the struggle ; or A will be able to turn out B, for instance, from the young leaves, and B turn out A from the old leaves ; A will be found feeding only on young leaves, B on old—there will be splitting of the common environment.

In neither case can this competition in a common environment be a factor in evolution.

Before proceeding further it is necessary to review the conclusions that have been made.

1. The boundaries of the environment of a species are definite.

2. The competition between species and species leads to either extinction of one or the splitting of the common environment into

two specific environments. Species generally occupy common environments without competition because there is no crowding there. Common environments do not give rise to specific structures.

3. New species are formed by differentiation of their specific environments.

4. The environment becomes similarly sexually and socially differentiated.

5. Change in environment will produce either evolution or degeneration. If ontogeny and phylogeny give the history of a species, they should also give the history of its environment.

The earliest forms of life were probably all aquatic. The embryos of nearly all vertebrates and invertebrates have some characters and structures which indicate that their distant ancestors lived in water.

The conceptions or confessions of faith embodied in most of the above arguments are of course not new; they have been recalled because they lead the way to the subject under consideration, namely, the power of enemies as selecting agents.

Particular attention is directed to conclusions Nos. 2 and 3, which state that common environments do not give rise to specific structures, or in other words, the

selection of common environments is, *re* evolution and the origin of species, of much less importance than the selection of specific environments.

Specific environments can often be recognised by their being usually restricted. The environment which restricts a species is a part of its specific environment. This will be found to be in the vast majority of cases either food supply or enemies. Food supply and enemies are closely connected ; if one is important, both must be. A is the food supply of B : B is the enemy of A. The greatest disturbances which man has made in Nature have been due to alterations in one of these two factors. The two most efficient ways of either exterminating a species or controlling it are the destruction of its food supply or the increase of its enemies. In Nature's balance the weights are these two factors.

Isolation is probably the greatest determining factor in the preservation of species. It ensures protection from fresh enemies. Migration the greatest determining factor in the destruction of species. It introduces new enemies. Species with many enemies are the least variable. Protection from enemies causes species to vary, as in domesticated animals.

It is possible to arrive at the same conclusion in other ways. There is evidence that the destruction of wild animals is in many respects similar to that observed in man: and that an animal life-table is very like a human one. Many are born to die almost at once: some die before reaching maturity; others become adults; and a few only reach old age. It has therefore been said that Natural Selection acts chiefly upon the young, and therefore must be most effective before the assumption of adult characters: and thus cannot be a powerful force in Evolution. But this is a false argument, apart from consideration of juvenile characters. Consider one thousand individuals, and suppose that ten of these become reproductively mature; then it is obvious that the death of one of these ten will be equivalent to the destruction of one hundred newly born individuals; which means that the power of Natural Selection, *re* Evolution, when adults are operated upon, is a hundred times as great as when newly born individuals are dealt with, and still greater when the adults are about to reproduce. It follows, therefore, that the factors which decide life or death of adults are very important ones of Natural Selection.

Evidence will now be brought forward that the most important of the selecting factors, the one always at work, is the species' enemies.

Consider temperature ; a severe winter kills off those with poor resisting power to cold ; then summer's drought comes, and another batch is destroyed. The following winter is mild, so the next generation are not subjected to selection by cold. A very hot summer destroys many of these, perhaps just those which are able to best resist cold : so that any advance in ability to resist cold, as a result of the first selection, will be lost, on account of the inconstancy of the selecting agent and the swamping effects of the other agents. But with enemies, the case is different ; they are always present, destroying through all the year ; and their action will be accumulative.

There is a property of enemies that requires to be especially mentioned. They destroy suddenly. There is no time for the species to protect itself by means of acquired characters. This power which enables organic matter to adapt itself to diversities of environment is valueless in respect of enemies : only hereditary characters can be used for this purpose. Therefore, as hereditary characters

usually form specific characters and acquired characters do not, it follows that the characters to do with protection from enemies are likely to be very important ones.

Much criticism has been levelled against natural selection from a mathematical point of view, and especially as regards the swamping effects of chance. If chance kills off 950 of a 1000 individuals, then natural selection has 50 instead of 1000 to work with. However, the effect must be the same, except that longer time will be required for the origin of favourable variations. When, however, after perhaps many generations the favourable variation does arise and escape the hands of chance, then it will be one amongst 50 instead of one in 1000, and therefore less likely to be swamped.

False examples of chance are often cited. The stepping of a horse on an ant's nest is a typical one. The action of the horse may be the result of chance. But what can be said about the position of the nest? The mother ant in the past chose this particular spot for her nest. Other mothers chose in some cases no doubt places where horses are not likely to walk. Will not such mothers therefore be thus selected to carry on the race?

In conclusion it may be said that, although the subject has been approached from several standpoints, reasoning has led in each case to the same two conclusions :

1. Specific environments are more important than common environments as selecting agents.

2. Species' enemies are very important

factors of specific environments: and must be powerful selecting agents calling forth important corresponding structures.

One other conclusion that has been arrived at may here be mentioned.

As has been truly pointed out, the welfare of a species is almost of as much importance to the species' enemy as to the species itself. In spite of this, some naturalists expect to find highly protectively coloured animals almost free from enemies. Were this so, then there would be no selection, there would be nothing to maintain this specialisation, which according to present-day arguments would at once begin to degenerate until its efficacy failed, permitting the enemy to again destroy.

It seems, therefore, that the most efficient protective coloration can only be maintained by a severe selection by enemies. So only can be produced and maintained other highly specialised characters such as warning coloration.

One must therefore expect to observe that animals which present a high degree of protective or warning coloration, frequently form food for their predaceous enemies.

CHAPTER V

FAMILY INSTINCTS

It may appear strange that instincts are first chosen to illustrate this Theory, for of all characters they are the least known or understood, and only in recent years have they been systematically studied, and been given an important place among characters as a whole.

They have been chosen because, as family characters, they well and clearly illustrate the Theory.

The vast majority of parents have an instinct which compels them to sacrifice themselves for the sake of their young; this sacrificing instinct is present in both sexes, and varies according to the age of the young. When the progeny is very young it is strongest, and as it grows older so the instinct becomes less strong: finally, when the progeny is full grown, it entirely ceases, and in many cases is replaced by another instinct, which compels the parents to drive away their progeny. The

possession of this parental instinct has an effect on the selection of enemies within the family : the likelihood of their selecting young is much reduced. As has been shown, young are more valuable to the species than old ; therefore the species controls Natural Selection in such a way, that more valuable young are preserved at the expense of less valuable parents. Families having this character are more likely to bring their young to maturity, and to thus reproduce themselves, than families in which this parental character is faint or absent.

Thus, the FAMILY comes to possess this character which has arisen as a variation and has been preserved through heredity : just as within the individual, particular forms, structures, or colours or other character having been born, becomes fixed.

Natural Selection, dealing with families, produces family characters whose function is to preserve the more valuable members of the family, at the expense of the less valuable.

To return to parental instincts, closely allied to the sacrificing instinct is a combative one. Parents will attack an enemy of their young. If they prove victorious, the instinct which directed their actions may be called combative ;

if they are beaten in the fight, it will be called sacrificing.

There is another parental instinct, commonly found in birds, which may be called an attracting instinct. It consists of unusual and conspicuous movements whose object is to distract an enemy from their young and entice it to attack the parents ; these are often described as feints because the birds appear to pretend to have broken legs or wings, or to be otherwise wounded and crippled. By these attracting instincts the parents draw an enemy's attack, and having accomplished this, then make good their own escape. During these feints, several ways of making themselves conspicuous are utilised : bright colours are displayed ; wings, wherein are bright bars, are opened ; tails containing white feathers are spread ; breasts or backs are turned, according as they are brightly coloured, towards the enemy. Strange forms are assumed ; combs are erected, tails spread, wings opened and necks thrown out ; and conspicuous sounds are made. By these and other methods, parents make themselves conspicuous.

When pre-copulatory displays are considered, it will be shown what a close similarity there is between these parental displays, these attracting instincts, and the dis-

plays made before copulation, which are usually called the displays of courtship. It will be further shown that, whereas the parental displays are to protect the young, the sexual displays of the male are to protect the female.

Whilst the parents are responding to these instincts, the young are behaving quite differently. Reacting to a warning of danger, given (either vocally or by other ways) to them by the parents, they instinctively make themselves as inconspicuous as possible : they at once squat or seek cover. This family character possessed by the young must control Natural Selection within the family, just as the parental instincts do. The young of a family who instinctively seek cover, when warned by the parents, have a better chance of surviving and of reproducing themselves, than the young who do not thus respond to their parents' call.

In like manner can be accounted for very many of the instincts found confined to parents, and those possessed solely by the young. Further, as will be shown later, many of the characters found confined to either parent or young, no matter what their nature, either structure, form, or colour, can be similarly explained.

Instincts have been chosen first for con-

sideration because they are self-evidently a means whereby Natural Selection within a family is controlled.

Many account for the parental sacrificing instinct by concluding that the young and the juvenile, because they are helpless and inexperienced in defence, require protection of their parents. But such an argument is not sound. They require protection because they are valuable to the species: their helplessness adds nothing to their value. However, apart from this question: the origin of these characters as variations confined to particular members of a society and their fixation, must have been through Natural Selection dealing with families, and not with individuals; and further, these characters must control Natural Selection in such a way that one set of individuals, the young, is rendered more liable to be selected for survival than the other, the parents.

.

CHAPTER VI

THE COPULATORY ATTITUDES OF THE PAIR

ANIMALS form themselves into a number of different societies. In the last chapter, the society of a family was considered in respect of one of its characters, its instincts ; another society has now to occupy the mind—the pair, the associated male and female. There is probably no society in Nature more close than the copulating pair. And because the pair thus united are especially open to attack, Natural Selection will probably leave its mark on these two individuals. As has been clearly proved, females are more valuable than males ; search should therefore reveal the presence of characters in the pair, which control Natural Selection in such a way that during copulation females will be preserved at the expense of males.

At present, only one character of the copulating pair will be dealt with—the attitudes they assume during copulation. A

hasty consideration might lead to the expression of opinion that copulatory attitudes depended on the position, structure, and mechanism of the copulatory organs : but the facts of Nature lead one to argue that she does not mould organs and then leave the individual to fit them as best he can ; instead, one is encouraged to believe that organs are made for use in a particular way. The question that is now asked is—Do the copulatory attitudes assumed by animals, in any way assist in the preservation of the female at the expense of the male ?

In mammals and birds, the position of the male above and behind the female must undoubtedly render him, in the event of an attack by an enemy, far more liable to be killed. A couple are especially liable to be successfully attacked from behind ; a frontal attack would be in their full view and likely to fail. A hawk stooping at a pair of birds, must strike the male. In mammals, the male, standing on his hind legs, is helpless compared to the female, who, standing on all four, is able to spring aside on the instant. Further, experience has taught predatory animals that it is unwise to leave a stricken victim until it is certainly dead ; for this reason, seldom

more than one of a pair is likely to be killed in an attack. The male's death is nothing to the species, for he probably has already fertilised the female, if not during the last copulation, at a former one; her death would be a great loss to the species, the loss of very valuable fertilised ova.

The length of time taken by the copulatory act varies with the species, and among mammals is longest in the predatory ones; compare, in this respect, the Felidæ Canidæ and Mustelidæ with the Suidæ, Cervidæ Equidæ or Muridæ and Leporidæ.

Among birds, I am aware of only one exception to the rule that the male mounts the hen—Swans (*Cygnus olor*), which copulate breast to breast, and so will apparently be equally liable to be killed if then attacked. It is noteworthy, that of all birds, Swans are probably the least liable to attack, because of their pugnacity and great strength.

In the majority of insects, the copulatory period is often prolonged for many hours or even days; during this long period the pairs are in a helpless condition, able only to make feeble attempts to escape from danger. In many species, the male rests on top of the female, as it were guarding her and often

carrying her in flight. In other species, the pairs unite end to end ; in these cases, other methods encouraging the taking of the male are utilised, as will be shown later. But although it seems that when thus united, an enemy would chance to take male and female equally, in many cases, owing to the position in space occupied by the copulating pair, this is not so ; for instance, in some cases the male clings to a grass stem or other support, whilst the female dangles below ; a bird taking such a pair will strike first where the insect joins the grass, having learnt by experience that of insects, this, the head end, is the most vulnerable part ; the bird will seize the male, the female becoming unjoined will be likely to escape. In such ways as this, by the assumption of a particular position on the part of the pair, will the taking of males rather than females be encouraged.

When copulating insects are given to birds, it has been observed that when one has been seized, the other is apparently mistaken by the bird for some foreign object, which the bird endeavours to and does get rid of by rapidly shaking its head : those insects which are firmly joined together and only with difficulty parted will thus be disconnected.

The copulating habits of the Common

Sparrow (*Passer domesticus*) are worthy of mention. Whilst the successful male is performing the act, the pair are usually closely surrounded by a number of chattering males. If this company of birds be attacked, it is not likely that the female will be taken, but rather one of the many males. I have twice seen a Hawk take a Sparrow under these conditions, and on each occasion it was a male. These two observations of course prove nothing, but, at the same time, it appeared to me to be impossible for the hawk to chance to take the female; a chance greater than the relative number of males to females.

So with certain insects, in which, during copulation, the pairs are surrounded by a host of males, these must protect the female, whether this be the aim of such a gathering or no. The above applies to many Diptera, the Bees (*Apiariæ*), Termidæ, and others.

Lastly, in bisexual or hermaphrodite animals, there is no difference in the relative position of the two individuals as would be expected according to the Theory, for they are of the same value. During copulation, they always make a symmetrical figure.

Thus in conclusion it may, I think, be fairly stated that the position assumed by the pair

during copulation renders males more liable to destruction than females. In this way the species may be said to control Natural Selection, so that valueless males may be destroyed rather than valuable females.

CHAPTER VII

PRE-COPULATORY DISPLAYS

BEFORE copulation, the male commonly makes some display ; such are often called the displays of courtship, implying an association with mating ; but as many animals mate only once in a lifetime or in a season, whilst these displays are made before each copulation, they are better described by being called Pre-copulatory Displays. A study of them shows that they undoubtedly render the male conspicuous and purposely so. All the methods mentioned in Chapters II and III are employed : movements are made, forms assumed, attitudes struck, sounds produced, scents secreted and vivid colours are laid bare, all of which make the male conspicuous in Nature. The female, during this display of the male, remains silent and motionless, and usually more or less concealed.

Here, then, is material to which the Theory can be applied : Two individuals, male and

female, unequal in value, associated together, and at a time when the difference in their values is greatest, *i.e.* during the breeding season; the male, the less valuable, renders himself conspicuous in many ways; the female keeps more or less concealed. Here are two associated individuals of different value, presenting different characters. According to the Theory, these characters, or at least some of them, should control Natural Selection in such a way that the less valuable male will be taken, rather than the more valuable female. Further, at this time, the pair are especially liable to be successfully attacked, because their attention is fully occupied with sexual affairs; so that some provision for the selection of the male may be expected. Therefore may it not be, that the male renders himself conspicuous in order that, in the event of the pair being attacked by an enemy, he may be destroyed rather than the female? The Hawk will stoop, the Cat will spring, at the more easily seen bird. It does not follow that one of the two must in every case perish; the display of the male will draw the attack of any neighbouring enemy and thus, as it were, clear the air, so that dangerous copulation may be accomplished in safety.

This, in fact, is the meaning of such display, its purpose.

Direct evidence of this is, and possibly must always be, wanting.

The period of destruction of an animal forms so minute a portion of its whole life, that a single person, even if constantly observing, could record only a few deaths, and of these only a small percentage would be deaths of either male or female during sexual display. Experiments could be arranged to test the theory. Pairs of animals could be subjected to their enemies.

Although direct evidence is wanting, some indirect evidence appears to give support. To the vast majority of animals man is an enemy. His presence causes them to stop doing the affair of the day, and to seek cover. But his presence often does not cause the cessation of pre-copulatory displays; on the other hand it may cause them to be more vigorously performed. In fact his presence calls forth this male reaction as powerfully as the presence of the female. Numerous examples have been recorded of display in the absence of the female, and when only man or an enemy is at hand.

Another favouring fact is that animals, not liable to be attacked, either make no pre-copulatory displays or only poor ones. It is also noteworthy that the displays made by the parents for the protection of their young during the attack of an enemy, are very similar to and sometimes exactly like pre-copulatory displays. In one case an enemy is the stimulating agent ; may it not be so in both ?

Just as there is no direct evidence in favour of this conception, so there is none against it. Other theories have been propounded to account for the facts ; these will be discussed under Sexual Colour (Chapter VIII) ; and what contrary indirect evidence there is will be also then considered.

Some have likened these displays to carresses, and have supposed that by them the male overcomes a coyness of the female. Females appear to be coy because they take no notice of the male's display ; for this reason, when the male's display appears to be kindly in nature towards the female, it is called a caress ; and no heed is taken of the many cases in which the male's display appears quite brutal. Further, much coyness on the part of the

female must, one would think, be harmful to the species.

This explanation therefore appears unsatisfactory, even for the small number of displays which it could account for.

CHAPTER VIII

SEXUAL COLOUR

MALES and females are frequently coloured differently. With comparatively few exceptions, the males are more brightly coloured, especially during the breeding season. These characters are widely distributed throughout the animal kingdom, and this universality indicates that the cause must be of a world-wide nature. In some cases it has been observed that the sexes occupy either entirely, or somewhat different, environments, hence their colour differences.

But in other cases, environmental differences, corresponding to these colour and other structural differences, have not been found. For this reason other theories have been propounded to account for them.

Darwin's sexual selection is the most generally accepted theory. This states that females select males which have characters pleasing to them, bright colours for instance. Assume

that this is so and that males in this way become altered in character. Such a male character must be either beneficial or detrimental to the species as a whole ; it cannot be neutral. If detrimental, the species must either become extinct, or Natural Selection will remove the offending character ; if beneficial, then Natural Selection would have fixed the male's useful variation without the assistance of female selection. Characters, confined to the male, can be fixed by Natural Selection alone, and thus selection on the part of the female is not necessary to explain their origin. In order that females, by selection, may alter the characters of males, two monosexual variations (one in the male, the other in the female) must arise simultaneously, and further, these must be related. For instance, a bright colour must arise as a variation in the male, and at the same time there must be born in the female as a variation, an instinct which compels her to prefer this bright-coloured male. To conceive of this is difficult.

On the other hand, Natural Selection would require only one variation to arise. If a beneficial character arises, it will become fixed, although the variation be confined to

one sex ; this conception is easier. Such a variation would be correlated with the sexual determinant ; variations not so correlated or bound to a sexual determinant cannot, one would conceive, be made to do so by Natural Selection : for instance, favour their fixation in the male, and their eradication in the female.

Sexual Selection, if it explains the origin of extra sexual characters, does not explain their use, yet, as has just been shown, they must be useful, or otherwise Natural Selection would remove them.

Beside this argument, there are many facts that sexual selection fails to correlate and which it ought to correlate. They mostly come under the following headings :

1. Sex selection accounts for the brilliant colours of males, but fails to account for equally brilliant colours which are frequently found in both sexes.

2. Sexual selection, if it has been observed, has not been observed to be especially associated with animals which show the greatest sexual differences in characters. Birds, for instance, in which the sexes are similar, do not show less selection by the female of the male, than birds whose males are of

the most brilliant colour compared to their females.

3. If females select then, there must be either more males than females or polygamy : but in many insects which present marked sexual differences, males and females are equal in number. Further, very few examples of selection by females have been recorded ; whereas many experiments have been carried out that conclusively show that females do not select.

4. In many animals, the male undoubtedly selects the female, and yet the male is the more brightly coloured.

5. The displays of courtship are not to do with mating, but, as has been shown, are pre-copulatory displays ; they therefore do not play the rôle in sexual selection which is assigned to them.

6. Further, these displays are not made only by animals which present secondary sexual differences in characters, but are also made by animals whose sexes are similar.

7. Sexual selection does not explain the absence of conspicuous male colouring in predatory and night animals ; or rather they form unexplained exceptions.

Of course there must be many facts which

the theory of sexual selection explains or correlates, else it could never have been conceived. Nevertheless much has been written against sexual selection, especially in Germany and America, and a general demand made for another explanation.¹ There are other theories. Wallace explains the dull dresses of female birds and insects by supposing that the young-producing females require better protection than the males. But one would think that if dull plumes are an advantage to the female they would also be of use to the male, and that therefore he would don them too. This theory of Wallace apparently comes very near to the one under description, but in reality it is almost the converse. The new theory states that the male becomes brilliant in colour in order that he may be more likely to be destroyed: and thus the dull-coloured female gain protection. In Wallace's theory the female becomes altered for her sake, in this theory the male for the female's sake. Wallace

¹ The author's theory is not, strictly speaking, antagonistic to Sexual Selection, but only in so far that such selection cannot be for the purpose of gratifying the female's sense of beauty. The new theory is quite able to embrace female selection provided they instinctively select males which will be more attractive to enemies than males in general; for instance, conspicuously coloured males as against beautiful males.

explains the dull colour of females but not the brilliant colour of males.

Emery's theory of the origin of secondary sexual characters as mono-sexual sports may explain their origin, although there appears to be little evidence of this, but makes no attempt to define the cause of these differences; or assumes that the sport is retained because and when it fits the environment better than the old type.

Those who believe in the transmission of acquired characters look upon secondary sexual characters as adaptations and due to the stimulation of parts through use. Controlled natural selection accounts for both the origin and purpose of secondary sexual characters in the following way. Males are more conspicuous in nature than females: males are less valuable than females. Males and females are associated together during life, and especially during the breeding season when the difference in colour is greatest, and when their difference in value is highest: therefore according to the theory, the conspicuous colour of the male serves to control natural selection in such a way that the less valuable male will be killed in preference to the more valuable female.

The occurrence of only a single variation is necessary for this conception. Because females who happen to choose the most conspicuous males, will be more liable to escape destruction than females who happen to be mated with less conspicuous males: and the former females will therefore be more likely to hand on this male character than the latter females. This applies to all the purposely conspicuous characters of males.

Stolzmann in 1885 put forward a theory to account for the secondary sexual characters of birds, which in some respects resembles this theory.

Having observed that males are often more numerous than females, he justly concluded that the species' food supply was being wasted on them and that this excess of males was harmful to the species; more especially because he believed that the paired females during the breeding season were harried by celibate males, with injurious results. He therefore conceived that the brilliant colours of the males arose in order that they might easily be seen by enemies and their ranks thus thinned.

This theory was very short-lived, because it was speedily pointed out, that if males

become conspicuous in order to be killed, only less conspicuous ones will be left to carry on the species, and conspicuousness will thus be quickly eradicated by Natural Selection.

It is obvious that this criticism cannot be levelled at the author's theory, which in some respects is not unlike Stolzmann's. The author's theory deals with the pair, male and female associated together at the breeding season or during copulation ; under these conditions the destruction of a conspicuous male by no means precludes that his characters will not be handed down to the next generation. He most probably will have already fertilised the female either partially or entirely. It may here be noted that secondary sexual characters are at their highest development at the time when the female is ready to be fertilised ; male birds, for instance, are in their most brilliant plumage, not during their nesting season, but at a considerable time before this, in either the last of winter or the first of spring.

The relative proportion of males to females is, as Stolzmann concludes, a most important factor in the welfare of the species. According to the theory, great excess of males

should be associated with great secondary sexual difference, and vice versa.

In some animals, an excess of males is produced by special methods, *e.g.* ants and bees. It appears not so much to ensure the fertilisation of all females, as to render the chance of their destruction small. It is noteworthy that polygamy is usually associated with great secondary sexual differences; these latter, according to the theory, give rise to great destruction of males, hence the association, as in the peacock. In predatory animals, polygamy is very rare; as are also great secondary sexual differences.

If, as some maintain, the purpose of eye-spots in insects is to entice enemies to strike them, rather than more vulnerable parts: may not the eye-spots on the peacock's (*Pavo Cristatus*) tail be to entice an enemy away from the female, to draw its attack?

When considering the parental colouring of birds, it will be noted that confinement of conspicuous colouring to the male is associated with open-nesting habits. It is possible that, among birds, conspicuous colouring confined to the male arose in this way (Wallace), and that afterwards it has become greatly evolved by Natural Selection working with pairs. There is some evidence that open-

nesting cannot alone account for such great differentiation, for when males incubate, females are never more than slightly more conspicuously coloured. It appears, therefore, that the difference in value between the sexes, or some other factor, must be looked for to explain this.

As with parental colour, so with sexual colour — conspicuous colours among predatory animals, or among night animals, would not be anticipated, nor is it found.

So also sexual dimorphism should, according to the theory, not be found in aposematic animals, nor is it at all common; because, having few enemies, they are not very liable to attack. Sometimes secondary sexual characters occur before sexual maturity, as in the upland Goose (*Chlaephaga Magellanica*). In this case one would conclude that the society feels the great value of the female even at this early stage.

Worthy of note and favouring the theory is the fact that in mimicry it is often only the female which seeks protection in this way; the male, it would seem, purposely refraining from doing so, in order that, should the pair be attacked during mating or copulation, he will be destroyed at the saving of the female.

Finally, it will be well to classify secondary sexual characters in the light of this new theory.

MONO-SEXUAL CHARACTERS :

1. Characters that are adaptations to a mono-sexual environment ; for instance, associated with a food supply confined to one sex, with copulation, with the rearing of young, with the recognition or finding of one sex by the other, &c.

2. Characters whose purpose is to control Natural Selection within the pair, value marks ; for instance, attracting colour, sound, scent, &c. confined to the male.

It must be clearly understood that the second cause of mono-sexual characters is, like the first, an environmental character. It is the result of selection by enemies, which selection has been shown to be one of the most important factors of a species' specific environment. For this reason it should not, theoretically, be given a major heading in the classification of the causes of mono-sexual characters. There is, however, a side issue which to some extent justifies this arrangement ; for the species behaves towards enemies in a particular manner.

It adjusts this selection by enemies so that,

when the members of a species are not all of equal value, the less valuable will be more likely to be destroyed than the more valuable.

It is as if the species, realising that it must form the food supply of another species and that certain of its members must be destroyed, conserved its valuable members, by casting its valueless ones to satisfy the enemy.

This it does, not actively but passively, by so clothing the valueless that they will be more easily seen by the enemy and thus more liable to be attacked.

As before mentioned, it does not follow that in every case they will be destroyed, they may make good their escape; but by drawing the attack, the valuable will be preserved from attack.

Further, it is obvious that there will be a limit to this value marking: as, for instance, when males become less numerous than females, so their relative value will increase; they are not entirely valueless.

When they thus become of equal value as the female, further alteration in structure will cease.

The limit to which this differentiation will proceed, will depend on the number of females a single male is able to fertilise, or his initial

value to the species in other respects. The greater the polygamy the greater the sexual difference, should be the rule. This, I think, most will agree, is borne out in Nature. Thus it appears that sexual differentiation is frequently an expression of selection by enemies.

CHAPTER IX

PARENTAL COLOUR

A COMPARISON of the colour of parents and young shows, that whereas young are almost invariably protectively coloured, parents are not uncommonly conspicuously coloured. This difference in colour is explained by some, who say that the protective colouring of young animals is the colour of their ancestors, which they *must* assume during development, because development reproduces the ancestry of the species : and who say that protective colouring must therefore be assumed, whether beneficial or not : and who look upon the conspicuous colouring of many adults as a more recent added character.

There is no doubt that an animal, during development, does reproduce its ancestry, but then there is *no* evidence that it *must* do so. Not all the characters of its ancestors are retained, but only a few : and of the few, many do not attain to as high a development as

was present in the ancestors. Is it not reasonable to suppose that only those characters are retained which are useful, or that of a given character only so much as is useful: or else why are so many completely lost?

The Tadpole (*Rana temporaria*) has first external gills, then internal gills, and finally lungs, all of which are put to use: so too it is possible that the gill clefts or their rudiments found in the human embryo then serve some useful purpose. Natural Selection must deal with ova, embryos, juveniles, as it does with adults, and produce embryonic or juvenile characters. Ova and embryos, like adults, have environments to which they must adapt themselves.

We are accustomed to study chiefly adult characters and to forget that adult is but a stage, merging on the one side into youth, and on the other, old age; each of which have important characters. Some of the characters of old age may be looked upon as means by which the species rids itself of an individual which has shed all its germ cells.

Selection must occur with reference to a character, at the time of, or after, the appearance of the character, and not before. Thus the characters that go to form an embryo or

young animal, or an adult, are of two kinds—(1) structures, or parts of structures, which their ancestors possessed, and which have been retained because they are useful; (2) added structures, which their distant ancestors never possessed, to fit some new environment; these may be added at any stage of development from the egg to the complete adult. Therefore the hereditary explanation of the difference of colour between young and adult is not sufficient. That this is so is also proved by the whole of experimental embryology, and also by the fact that examples can be found of young animals not presenting protective colouring, and almost certainly not having the colour of their ancestors. One must conclude, therefore, that young animals are as a rule protectively coloured, and adults often conspicuously coloured, for a purpose.

An examination of the species which present protectively coloured young and conspicuously coloured adults, reveals the fact that in the vast majority of cases young and parents are associated together during a portion of their lives; and further, that it is whilst thus associated that the difference is most marked—*e.g.* parents are most brilliant during the breeding season. Examples of conspicuously

coloured parents and protectively coloured young are to be found widely distributed in the animal kingdom. In fact, it is exceptional to find parents, bringing up young, which do not show this difference in colour or other character. Thus are brought together the three factors with which Controlled Natural Selection can work :

- (1) A society of animals
- (2) Of different value, and
- (3) Having different characters.

During Natural Selection the less valuable and conspicuous parents will be taken, at the saving of the more valuable and inconspicuous young. The predatory animal will take the conspicuous parents that it can best see, and leave the young that are only seen with difficulty.

When dealing with Parental Instincts, mention was made of the displays of colour that are made by the parent when the family is attacked; they will show their brightest plumes to the enemy and endeavour to draw its attack ; they will display bright colours which are otherwise concealed in wings and tail (see Concealed Conspicuous Colours, Chapter III).

Predatory animals, because they have no enemies, should not present conspicuous colour-

ing, neither do they ; they are almost always protectively coloured.

For instance, of the Falconidæ, only the small insectivorous species that are liable to be attacked by the more powerful kinds show conspicuous colouring. For similar reasons, no night birds should present, nor do they, conspicuous colouring. There are, however, many birds which present conspicuous colouring only in the male : with very few exceptions these are found to make open nests, which require the female to be protectively coloured ; for this reason, only the male is conspicuously coloured (when males incubate, females are the more conspicuous). There still remain many which are neither predatory nor night birds, and which, nevertheless, are protectively coloured in both sexes ; it is among these birds that conspicuous displays are seen best, and most marked. The position these birds will take up, the motion they will make in an endeavour thus to protect their young, are remarkable—the Meadow-pipit (*Anthus pratensis*), the Reed-bunting (*Emberiza schæniclus*), and the Partridge (*Perdix cinerea*) are well-known examples. Only by the collection of a large number of facts such as these can the theory become a law. As before mentioned,

it is now only being introduced as a working hypothesis. It will probably not explain all cases of conspicuous colouring among parents, for it has been shown that conspicuous colouring may be used for other purposes.

Attraction marks (see page 40, Chapter III) may be especially mentioned, for although they are conspicuous they are found in both parents and young. The rule appears to be: (1) vital parts that are conspicuously coloured in parents are protectively coloured in young, and (2) non-vital parts conspicuously coloured in parents are similarly coloured in young.

A few examples are necessary: (1) The Goldfinch (*Carduelis elegans*): yellow bar across the wing, found in both parents and young; other conspicuous colours on vital parts of parents are not found in young, which are protectively coloured; (2) Wheat-ear (*Saxicola ænanthe*): white rump present in both parents and young; (3) Wood-pigeon (*Columba palumbus*): white patch on side of neck in parent, and because on a vital part, not present in young; (4) Mallard (*Anasbascus*): speculum on wing found in young and old, in all plumages.

It appears, therefore, that some of the differences in colour between parents and young,

like the differences between male and female, may be due to the selection of enemies working on individuals of different value ; may in fact be on one hand value marks, and on the other adaptation to enemies.

CHAPTER X

PARENTAL AND SEXUAL CHARACTERS

MENTION has been made that among birds, for instance, there are many which do not present conspicuous colouring, in either sex. It has also been shown (under parental instincts) how these birds protect their young by making themselves conspicuous other than by means of colour; similarly it has been noted that female protection is accomplished in these birds by pre-copulatory displays on the part of the male, quite apart from colour. In these cryptically coloured birds, another male character is also possibly used for female protection, namely—Song.

The production of sounds during pre-copulatory displays are obviously a part of the display. But the songs of birds cannot be thus classed.

Singing birds are conspicuous in nature,

and there is considerable evidence that they always sing for this purpose. When performing, the males invariably take up prominent positions, the tops of trees, high in the air, on the summits of rocks, &c., whence they may easily be seen from all around. Further, many of them sing when disturbed or frightened by an enemy; a stone cast into a reed-bed or thicket will at once start the warblers in full chorus. They sing in the morning and evening when predatory animals are feeding. They sing when a hawk or weasel shows itself in the copse. They do not sing to their females, who may be out of hearing, and who take no notice of the song, but proceed with the affairs of the day, unaffected. May not this male character be brought into the line which many other male characters have been considered to take, namely, that its purpose is to attract possible enemies, so that comparatively valueless males may perish, rather than their valuable females, or at least draw the enemy's attack?

The instrumentation of the males of insects may also be, in many cases, for this purpose. Sound-producing males are most commonly found in palatable insects.

Scent may similarly be used for female

protection ; the absence of scent in many hen birds which nest on the ground, indicates that scent plays a greater part in Nature than our feeble sense organ would lead us to imagine.

The pleasant perfume which some male insects have, may be to draw an enemy's attention to them, during copulation, rather than to the female. In offensively scented insects, the sexes are usually similar, and the character is probably of a warning nature.

This concludes the majority of the characters of conspicuousness which distinguish parents from young, male from female : in the one case, young as protected at the expense of parents ; in the other, females at the expense of males. The following table indicates how precisely similar are the methods used ; examples are given from among birds :

TABLE I

PROTECTION OF YOUNG BY PARENTS

	Position.	Form.	Movement.	Sound.	Scent.	Colour.
PARENTS	take up prominent positions:	erect plumes, spread tails and wings.	simulate injury, flutter, &c.	make various noises—the cackling hen.	(no examples found.)	display their bright plumes and have bright colours.
YOUNG	lie low, squat.	conceal their form.	remain quite motionless or retreat.	remain silent.	(no examples found.)	are cryptically coloured.
PROTECTION OF FEMALE BY MALE						
MALE	pre-copulatory attitudes.	pre-copulatory erection of plumes, &c.	many curious pre-copulatory movements.	pre-copulatory sounds, also songs.	does not lose scent: in many insects sweet-scented.	has attracting colour.
FEMALE	remains for the most part concealed.	hides form.	quiescent.	quiet.	scentless during breeding season.	is cryptically coloured.

If, as some will be willing to admit, the parents use these various ways for the pro-

tection of their young (instinctively), why should not similar performances and exhibitions on the part of the male, be to protect the female? A more detailed comparison of the means the parent uses to protect the young, with the pre-copulatory displays of the male, shows how strikingly similar are not only the methods used, but the actual movements, positions, and sounds, &c., made. In one case a given stimulus, the presence of an enemy coupled with possession of young, causes the parent to instinctively react; in the other a given stimulus, the presence of an enemy, either real or assumed, coupled with the sexual possession of a female, causes the male to react in a similar manner. And just as attracting instincts in both sexes serve to protect the young, and in the male to protect the female, so the attracting colour of parents and males will have the same effect.

Further, these displays, pre-copulatory and for young protection, are often made when neither females nor young are present, but at the approach of an enemy; they are then called expressions of fear, instead of reactions to a stimulus. May not this be the stimulus always, no matter when they are displayed?

For each species a table can be drawn up, like the above table of generalities ; for instance, in the case of a blackbird (*Turdus merula*) the following table results :

TABLE II

PROTECTION OF YOUNG BY PARENTS

	Position.	Form.	Movement.	Sound.	Scent.	Colour.
PARENTS	show themselves prominently in the hedge row.	droop wings, spread tails.	hop and flutter from branch to branch.	loud cackling noises.	nil.	male attracting colour.
YOUNG	remain concealed.	remain concealed.	remain still.	silent.	nil.	young cryptically coloured.
PROTECTION OF FEMALE BY MALE						
MALE	takes up prominent positions on trees, &c.	droops wings, and spreads tail.	hops and flutters from branch to branch.	incessant, loud cackling, and song.	nil.	has attracting colour (black).
FEMALE	does not do so.	does not alter form.	remains still.	silent.	nil.	cryptically coloured.

To this must be added the sacrificing and combative instincts which are used by the parents for the protection of the young, and by the male for the protection of the female. Female protection by this method is not very common in Nature ; the best examples are to be found in the higher animals, and especially those which live together in societies : herds are often thus protected by the males.

All possible combinations, of attracting and protecting colorations, will now be briefly considered.

C = conspicuous or attracting coloration.

I = inconspicuous or cryptically coloured.

P = parents.

Y = young.

P C Very common, especially in species
Y I which form themselves in societies of families ; but also rarely in other species in which the parents do not look after the young. To protect the more valuable young, in the latter case, in the absence of the formation of a society.

P I Almost unknown, and forming ex-
Y C ceptions to the rule. Examples can often be explained ; for instance, the young frog, the tadpole, when black and conspicuous, is not palatable.

P C By no means uncommon ; in the vast
Y C majority of these cases the conspicuous
 characters of the young are like those
 of the parents, and, like them, are of
 a warning nature.

P I A common condition when the species
Y I does not form itself into the society or
 family ; but when families are found,
 some conspicuous character is almost
 always found in the parents, which is
 not present in the young.

♂ *C* Is very common in all mono-sexual
 ♂ *I* animals : to protect the more valuable
 female.

♂ *I* Very rare and form exceptions to the
 ♂ *C* theory ; can sometimes be explained by
 their having unusual habits, as in the
 Phalaropes ; or by their being pro-
 tectively coloured to different environ-
 ments, although not at first sight
 obviously so.

♂ *C* Not uncommon, and almost always
 ♂ *C* the conspicuous characters are warning.

♂ *I* Not uncommon ; colour or form may
 ♂ *I* be similar in the two sexes and pro-
 tective, but they are seldom entirely

alike ; usually the male will be found to be conspicuous in one or more characters, as in song birds.

In conclusion it may be said that many, if not the majority of those characters which distinguish males from females, are similar to the differences found between parents and young.

Males equal females plus some other characters, females equal young plus some characters. In each case the added characters are alike, and according to the theory serve the same purpose.

CHAPTER XI

CONSIDERATION OF BRITISH BIRDS

IN order to demonstrate, in still more detail, the applicability of the theory, it will now be applied to the colour of adult British Birds during the breeding season. This material is chosen because it is better to treat a small amount of material exhaustively, than to pick out from a large quantity (aves) only favourable examples ; and because the habits and colours of British Birds are very well and widely known : also because birds, as a whole, are thus by no means badly exemplified ; and birds well exemplify the theory. They are classified in the following way, and will be considered accordingly :

1. Male and female
both cryptic	{	1. Birds of prey.
2. Night birds.
3. Song birds.
4. Other birds.
2. Female attracting
Male attracting	{	5. Open nests.
6. Closed nests.
3. Female cryptic
Male attracting	{	7. Open nests.
8. Closed nests.
4. Female attracting
Male cryptic	{	9. Open nests (2 birds).
10. Closed nests (nil).

The following method of placing the birds in the tables is employed. Birds presenting defined, unconcealed, flat areas of red, blue, yellow, black or white are placed under "attracting"; the rest under "cryptic." In a few cases difficulties arise; for instance, the Ring Dove (*C. palumbus*) has a small white patch on either side of the neck, and should therefore have been placed under "attracting": but because the area of white is, compared to the bird, very small, and the bird otherwise undoubtedly cryptically coloured, it has been placed under "cryptic."

DIVISION I

Birds of Prey.—See Table I.

Without exception, none of these birds present conspicuous colouring because they are not liable to be attacked. They require to be cryptically coloured so as to be able to approach their prey unobserved. The sexes are similar, therefore males are not especially destroyed, and polygamy does not occur.

Night Birds.—See Table II.

These are, without exception, cryptically coloured; attracting colour for the protection

of females and young would be useless, because at night it would be invisible to enemies.

Birds of Song.—See Table III.

In these birds, female protection is accomplished by means of the attracting songs of the males. The young are protected by the parents rendering themselves conspicuous in other ways; among these birds, the best examples of sacrificing and combative instincts and attracting motions and sounds, for the protection of young, are to be found.

Other Birds.—See Table IV.

The absence of conspicuous colouring in these birds cannot in all cases be explained. In the Divers, protection of young is not necessary, as these birds have always a retreat at their feet—the water. Others are in reality birds of song, although not so placed, *i.e.* the Curlew, the Whimbrel, Redshank, Common Sandpiper, Greenshank, the Doves, and the Wryneck. Some inhabit thick undergrowths, where conspicuous colours would not tell—Corncrake, Water-rail, and Hedge Sparrow.

In the Partridge, the young are protected by attracting movements of the parents, which in this bird are remarkable; but there seems to be no provision for the protection of the

female, except perhaps the habit the male has of always rising first, when the pair is flushed. In this bird, pre-copulatory displays are by no means wanting. There yet remain to be accounted for, the Greylag Goose, Sandmartin, Tree Sparrow, and Tree-creeper; something might be said of each, but controversial and therefore doubtful facts would have to be utilised.

DIVISION II

This division includes birds presenting bi-sexual attracting coloration for the protection of their cryptically, or much less brilliantly coloured young.

Many of these birds have a seasonal moult: in the winter, when they do not possess young, they don a cryptic dress. In some the change from juvenile to adult plumage is slow, and extends over several years: usually these full-grown but not maturely coloured birds do not breed, and therefore do not require attracting coloration for protection of young. Further, adult and immature birds often keep together, in companies, for several seasons, in which case the gradual change from juvenile to adult plumage would be a prolonged ad-

vantage, in that young would be constantly protected, as in the Gannet.

Although both the males and females of these birds are conspicuously coloured, the males are usually more conspicuous. This would make the males more powerful attracting agents than females. Other methods are of course also utilised.

There is evidence that some of these birds present warning coloration; for instance, powerful birds (Swan, Cormorant, &c.), and ill-flavoured birds (Petrels and Kingfisher).

DIVISION III

Comprises birds having purposely conspicuous or attracting coloration confined to the male. The vast majority of these birds (Table VII) make open nests, a habit that possibly causes the female to be cryptically coloured. Thus the male only has attractive coloration for the purpose of protecting the young. Arising in this way, this coloration is also used during the breeding season, for the protection of the female.

In the *analidæ*, the males usually take no part in the bringing up of the young, and yet the males are very conspicuously coloured during the breeding season; moreover, directly

the males desert the females, they become, by a post-nuptial moult, cryptically coloured. It appears probable, therefore, that the male coloration during the breeding season is for the purpose of protecting the female. In the other birds, the males assist in the rearing of the young and do not lose this conspicuous plumage, by means of a post-nuptial moult.

The following conceptions are thus arrived at :

1. The females are cryptically coloured because of the open-nesting habits.

2. The males retain attracting coloration for the purpose of protecting the young.

3. The difference in colour between the sexes thus arising, is also used during the breeding season, for the purpose of protecting the female.

Three birds which present sexual differences in colour, nest in closed nests : the Stonechat, Whinchat, and House Sparrow (Table VIII). In the case of the Stonechat and the Whinchat, it is probable that this nesting habit is a recent acquisition, for they lay blue and blue-green eggs, characteristic of open-nesting birds, and not the white eggs usually laid by closed-nesting birds ; further, although these nests are domed, the covering is frequently

scanty ; and in the case of the Sparrow, may be entirely absent. The dome of the Sparrow's nest is never well-made nor very complete.

It is necessary now to return to DIVISION II : " Birds having Conspicuous Colouring in Both Sexes."

As would be expected, the majority of these make closed nests. There are, however, some which make open ones but whose females are not cryptically coloured (see Table V) ; in some of these the conspicuous colouring is concealed whilst the hen is sitting (Table V, * birds) ; others are powerful birds, or birds which nest in colonies and whose females are not liable to be attacked whilst sitting (Table V, birds marked †).

Four birds, the Water-hen and the Coot, the Red- and Black-throated Divers, are able to leave their nests unobserved, and do so at the least alarm, so that it is very difficult to view these birds sitting.

In two birds, the Lapwing and the Oystercatcher, the male keeps guard over the sitting female and warns her on the approach of danger ; she is thus able to leave the nest when the enemy is far distant. Without opera glasses, it is difficult to view these birds whilst sitting.

For these several reasons, it is not necessary for the females of the above birds, although making open nests, to be cryptically coloured. This completes the list of British Birds, with the exception of the Phalaropes and Dotterel, in which the female sex is the more brightly coloured one. In these birds, the male incubates the eggs in an open nest, and so only the female retains the conspicuous colouring that is used for the protection of young.

One other fact is of some interest: many cases have been observed of females assuming male plumage; this change of plumage has been found to be associated with sterility; whatever the mechanism by which this is brought about, it is clearly, according to the theory, an advantage to the species. Males are more conspicuous than females because they are less valuable, therefore a sterile female, because she is less valuable than a fertile one, becomes conspicuous.

It will be well to review the facts which the theory correlates regarding the colour of British Birds: it accounts for

1. The presence of conspicuous colouring in both sexes.

2. The more conspicuous colouring of the male in these birds.

3. The presence of conspicuous colouring in the male only.

4. The absence of conspicuous colouring in preying birds.

5. The absence of conspicuous colouring in night birds.

6. The association of open-nesting with conspicuous males.

7. The post-nuptial change of plumage in the analidæ and its absence in other epigamic coloured birds.

8. The brighter colouring of the female in the Phalaropes and Dotterel.

9. The presence of cryptic colouring in females and young birds.

10. The older the bird, the more brightly coloured it is, as in the Gannet.

11. The female assuming male plumage, when rendered sterile by disease.

Thus can this hypothesis be applied to any selected material. In birds, it seems that protection of young is the most important factor in causing colour-differentiation in the society; had insects been chosen, the protection of females would have been seen to be a most important factor in sexual differentiation of colour.

When material is considered in this way, that is, exhaustively, discourse is confined almost entirely to exceptions. A wrong im-

pression of the utility of the theory is thereby obtained, because it appears necessary to so frequently strain it. Theories are usually substantiated by chosen facts. It is well, therefore, to state that 173 birds have been considered, and only a few have required to be reviewed.

TABLE I.—BIRDS OF PREY

Falconidæ	{	Marsh Harrier . .	Circus æruginosus
		Hen Harrier . .	C. cyaneus
		Montague's Harrier	C. cineraceus
		Buzzard	Buteo vulgaris
		Golden Eagle . .	Aquila chrysaetos
		White-tailed Eagle	Haliaeetus albicilla
		*Sparrow Hawk . .	Accipiter nisus
		Osprey	Pandion haliaetus
		Peregrine Falcon .	Falco peregrinus
		Merlin	F. aesalon
Stercorariinæ	{	Kestrel	Tinnunculus alaudarius
		Richardson's Skua	S. crepidatus
		Common Skua . .	S. catarrhactes
		Heron	Ardea cinerea

[* Mimicked by cuckoo, Cuculus canorus.]

TABLE II.—NIGHT BIRDS

Strigidæ	{	Barn Owl . . .	Strix flammea
		Long-eared Owl .	Asio otus
		Short-eared Owl .	A. brachyotus
		Tawny Owl . . .	Syrnium aluco
		Little Owl . . .	Athene noctua

Snipe	Gallinago cælestis
Woodcock	Scolopax rusticulus
Stone Curlew	Œdicnemus scolopax
Nightjar	Caprimulgus europæus
Bittern	Botaurus stellaris

TABLE III.—SONG BIRDS

Missel Thrush	Turdus viscivorus
Song Thrush	T. musicus
Nightingale	Daulias luscinia
Whitethroat	Sylvia cinerea
Lesser Whitethroat	S. curruca
Garden Warbler	S. hortensis
Dartford Warbler	Melizophilus undatus
Chiffchaff	Phylloscopus rufus
Willow Wren	P. trochilus
Wood Wren	P. sibilatrix
Reed Warbler	Acrocephalus streperus
Sedge Warbler	A. phragmitis
Grasshopper Warbler	Locustella nævia
Wren	Proglodytes parvulus
Meadow Pipit	Anthus pratensis
Tree Pipit	A. trivialis
Rock Pipit	A. obscurus
Skylark	Alauda arvensis
Woodlark	A. arborea
Corn Bunting	Emberiza miliaria

TABLE IV.—OTHER BIRDS

Hedge Sparrow	Accentor modularis
Spotted Flycatcher	Muscicapa grisol
Sand Martin	Cotili riparia
Tree Sparrow	Passer montanus

118 CONTROLLED NATURAL SELECTION

Tree Creeper . . .	<i>Certhia familiaris</i>
Wood Pigeon . . .	<i>Columba palumbus</i>
Stock Dove . . .	<i>C. œnas</i>
Rock Dove . . .	<i>C. livia</i>
Turtle Dove . . .	<i>Turtur communis</i>
Whimbrel . . .	<i>Numenius phœopus</i>
Curlew . . .	<i>N. arquata</i>
Common Sandpiper . . .	<i>Tringoides hypoleucus</i>
Redshank . . .	<i>Totanus calidris</i>
Greenshank . . .	<i>T. canescens</i>
Great Crested Grebe . . .	<i>Podiceps cristatus</i>
Little Grebe . . .	<i>Tachybaptus fluviatilis</i>
Common Guillemot . . .	<i>Lomvia triole</i>
Greylag Goose . . .	<i>Anser cinerrus</i>
Wryneck . . .	<i>Lynx torquilla</i>
Corncrake . . .	<i>Crex pratensis</i>
Partridge . . .	<i>Perdix cinerea</i>
Red Grouse . . .	<i>Tetrao scoticus</i>
Ptarmigan . . .	<i>T. mutus</i>
Water-rail . . .	<i>Rallus Aquaticus</i>

TABLE V

*Red-legged Partridge . . .	<i>Caccabio rufa</i>
*Dunlin . . .	<i>Tringa alpina</i>
*Golden Plover . . .	<i>Charadrius fluviialis</i>
*Ringed Plover . . .	<i>Ægialitis hiaticula</i>
*Ring Ouzel . . .	<i>Turdus torquatus</i>
*Kentish Plover . . .	<i>A. cantiana</i>
Lapwing . . .	<i>Vanellus vulgaris</i>
Water-hen . . .	<i>Gallinula chloropus</i>
Oyster Catcher . . .	<i>Hæmatopus ostralegus</i>
Coot . . .	<i>Fulica atra</i>
Black-throated Diver . . .	<i>Colymbus arcticus</i>
Red-throated Diver . . .	<i>C. Septemtrionalis</i>

Goldfinch . . .	<i>Carduelis elegans</i>
†Hawfinch . . .	<i>Coccothrauster vulgaris</i>
†Cormorant . . .	<i>Phalacrocorax carbo</i>
†Shag . . .	<i>P. graculus</i>
†Gannet . . .	<i>Sula bassana</i>
†Swan . . .	<i>Cygnus (olor)</i>
†Six Species of Gulls .	<i>Laridæ</i>
†Five Species of Terns .	<i>Laridæ</i>
†Razor Bill . . .	<i>Alea torda</i>
†Five Species of Corvidæ	
†Black Guillemot . . .	<i>Uria grylle</i>

TABLE VI

Swallow . . .	<i>Hirundo rustica</i>
House Martin . . .	<i>Chelidon urbica</i>
Pied Flycatcher . . .	<i>Muscieapa atricapilla</i>
Dipper . . .	<i>Cinclus aquaticus</i>
Redstart . . .	<i>Ruticilla phœnicurus</i>
Robin . . .	<i>Erithacus rubecula</i>
Pied Wagtail . . .	<i>Montacilla lugubris</i>
Wheatear . . .	<i>Saxicola œnanthe</i>
Five Species of Parinæ	
Gold Crest Wren . . .	<i>Regulus cristatus</i>
Nuthatch . . .	<i>Sitta cæsia</i>
Starling . . .	<i>Sturnus vulgaris</i>
Three Species of Corvidæ	
Swift . . .	<i>Cypselus apus</i>
Three Species of Picidæ	
Kingfisher . . .	<i>Alcedo ispida</i>
Merganser . . .	<i>Mergus serrator</i>
Goosander . . .	<i>M. merganser</i>
Sheldrake . . .	<i>Padorna cornuta</i>
Four Species of Turbinaris	
Puffin . . .	<i>Fratercula artica</i>

TABLE VII

Eider Duck . . .	<i>Somateria mollissima</i>
Mallard . . .	<i>Anas boscas</i>
Shoveller . . .	<i>Spatula clypeata</i>
Teal . . .	<i>Querquedula discors</i>
Pochard . . .	<i>Fuligula perina</i>
Golden Eye . . .	<i>F. clangula</i>
Gadwell . . .	<i>Chaulelasmus streperus</i>
Garganey . . .	<i>Q. cercia</i>
Tufted Duck . . .	<i>F. cristata</i>
Widgeon . . .	<i>Mareca penelope</i>
Pheasant . . .	<i>Phasianus colchicus</i>
Capercaillie . . .	<i>Tetrao urogallus</i>
Black Grouse . . .	<i>T. tetrix</i>
Greenfinch . . .	<i>Ligurinus chloris</i>
Siskin . . .	<i>Chrysometris spinus</i>
Chaffinch . . .	<i>Fringilla cœlebs</i>
Linnet . . .	<i>Linola cannabina</i>
Twite . . .	<i>F. flavirostris</i>
Lesser Redpoll . . .	<i>L. rufescens</i>
Bullfinch . . .	<i>Pyrrhula Europœa</i>
Yellow Bunting . . .	<i>Emberiza citrinella</i>
Crossbill . . .	<i>Loxia curvirostra</i>
Reed Bunting . . .	<i>E. schœniclus</i>
Blackbird . . .	<i>Turdus merula</i>
Cirl Bunting . . .	<i>E. cirrus</i>
Bearded Tit . . .	<i>Panurus biamicus</i>
Blackcap . . .	<i>Sylvia atricapilla</i>
Grey Wagtail . . .	<i>Motacilla melanope</i>
Red-backed Shrike . . .	<i>Lanius collurio</i>
Yellow Wagtail . . .	<i>M. rayii</i>

TABLE VIII

Stonechat . . .	Pratincola rubicola
Whinchat . . .	P. rubetra
House Sparrow . . .	Passer domesticus

TABLE IX

Phalarope and Dotterel

CHAPTER XII

HUMAN AND OTHER SOCIETIES

AT present only two societies have been dealt with, the Pair and the Family. Before, however, passing on to others, a few remarks will be made relevant to the Pair among insects.

In many insects the period of copulation extends over several hours and often over days. Moreover they are, during this period, quite defenceless and are able to utilise but poor means of escape. Therefore one would expect to find them exhibiting characters which would entice enemies to take males rather than females ; especially as the unnatural disjoining of pairs, even a short time after copulation has begun, does not result in an entirely infertile female, but in a more or less completely fertilised one.

In some cases the separating of the pair takes place immediately either male or female are seized, and especially the male ; in others

separation appears to be difficult or to require some time.

Observations show that unpalatable insects especially have this habit, but too few have been made to justify a definite statement. If this prove to be a fact, its meaning is clear—they do not require this method for the escape of either male or female, because they are not so liable to attack.

In this connection some observations, which have been made when birds are given copulating insects as food, have a bearing—one of the two copulating individuals is seized, but instead of both being at once swallowed, the bird for some reason almost always shakes or scrapes off the other. The impression gained is that the bird mistakes the second insect for an adherent foreign body.

It appears, therefore, that were the male of a copulating pair to be seized by a predatory animal, there would be considerable chance of the female escaping.

The following are methods of self-advertisement whereby male insects draw the attack of enemies :

1. *Position*.—Males rest on the top of the female and are therefore more likely to be seized. In many cases the males are very much larger than the females and completely

enclose them during copulation (the Cow-dung Fly).

In other cases, although not on top of the female, the males are more ready to hand because the pair takes up a particular position in space; for instance, the female may hang pendent from the male, this will encourage an enemy to seize the male: the bird would consider the point of suspension to be the head-end, and therefore seize this as being the most valuable part.

2. *Movement*.—When attempts at escape are made, it is almost invariably the rule that the male flies or runs carrying the female; in order to prevent escape, the bird will invariably strike at the moving parts, the male: where there is movement there is vulnerability (many *lepidoptera*). Even when actual escape is not attempted, the male will often make attracting flutterings of his wings when disturbed; this is a very common character (most *noctuæ*).

3. *Colour*.—Attracting colour in the male is common; when both sexes are conspicuous the colour is usually “warning.”

4. *Mimicry*.—It is common to find only females mimicking and thereby gaining protection. The absence of mimicry on the part

of the males renders them liable to be attacked.

5. *Sound*.—Males make sounds during copulation, especially when disturbed or captured.

6. *Scent*.—When both males and females are scented, the odour which they exhale is usually obnoxious and either advertises unpalatableness or renders them unpalatable. When males alone are scented they are perfumed ; this renders them especially attractive rather than repulsive.

7. *Dances* are often made by males, who thus render themselves open to attack. The females do not leave cover except for a moment to join the males and be fertilised. These are pre-copulatory displays similar to those found in birds. Will not the dances of the Bower Birds, the running in and out of the bower, the display of bright objects on the ground around the bower, draw the attack of enemies and clear the air for copulation ?

8. *Males* seek the females, thereby exposing themselves to enemies more than females. It seems, therefore, that the Theory is able to explain the vast number of secondary sexual characters of insects.

Other societies must now be considered, and first the Herd. Here, no new kind of indi-

vidual is found but a combination of sexually mature males and females, and young. This society differs from the Family, in that the onset of a breeding season does not break up the family formed at the previous breeding season.

In this society, males are always much less numerous than females, and thus the inferior value of the male is demonstrated.

Herd A, in which there are few males, is better off than Herd B, in which males and females are equal in number, because Herd A will require less of a limited food supply and yet have the same reproductive power.

Now, probably in all vertebrate animals, the sexes are more or less equal at birth: the question therefore arises—How does the species rid itself of these males in excess of the number required, which are not only useless but positively harmful? In the following ways:

1. By fighting among the males, the more powerful males destroy the less powerful. Herd A, whose males possess this instinct, will have an advantage over Herd B, whose males do not fight.

2. By the expulsion of males from the herd. The more powerful males, instead of destroy-

ing the less powerful, are sometimes satisfied by their banishment; the females may assist after a battle has declared the victors. The expelled males, without the protection of the herd, probably quickly fall victims to predatory animals.

3. By the destruction of males by females : this is not unknown.

4. By enemies more frequently destroying males than females because of their possessing "attracting" characters. When a herd is attacked the males, because they possess combative and sacrificing instincts, usually protect the young and the females, and must often thus themselves be destroyed.

If males and females were alike both in characters and instincts, as many females would be killed as males.

By these methods, Natural Selection within the herd is controlled. The adult male possesses special secondary sexual characters for purposes of offence and defence; the young males are like the females and do not present these characters, these offensive and defensive instincts, until sexually mature—this because young males are more valuable than old ones.

The attracting colour of male birds, which

live together in flocks, is not attained sometimes for several years.

Males, when at the zenith of their power, become monarchs of the herd for a season or two, and are then thrown out to die. Poor males never become monarchs. The percentage of males cannot be dangerously reduced by these methods, because the percentage of males to females at birth remains always the same.

In certain species of insects, especially in the Hymenoptera, another kind of society is found, composed of males, females, young and neuters or asexual females. In these societies, the actual production of males is controlled by the females and neuters; males are produced only when required, and after they have fertilised the young females they either die or are destroyed, the females and neuters alone remaining to carry on the species. (The males of these insects are not provided with weapons of offence—stings, &c.) Here, then, provisions are made not only for the destruction of males but for the limitation of their production.

Asexual reproduction in invertebrates, which is by no means rare, appears to be

for the same purpose, namely, in order that valuable food material may not be wasted on comparatively invaluable males. It seems that it is only owing to the necessity of occasional cross-fertilisation, that males are born at all.

Finally, Human Society may be briefly examined in the light of the new Theory. The fighting instincts of the male are perhaps better developed in man than in any lower animal. Primitive races were perpetually at war and valuable females were the prizes of war. Races were prosperous or otherwise, according as they were good fighters or not ; this resulted in polygamy and great power of reproduction. To-day, the more civilised races do not fight and are therefore not polygamous. The reproductive power of the races of to-day is therefore much curtailed and the relative value of the female very much increased.

Besides the fighting instinct, the male has a strong instinct to protect females even at the expense of his life, and both males and females have a similar instinct with regard to their children. The habit which the males of savage races have of rendering themselves conspicuous by paint and feathers, may be in

order to make themselves easily visible to their enemies, other tribes. It must be remembered that savage man delighted in fighting; he did not seek always to take his enemy unawares, but rather desired to meet him in fair and open battle.

There appears to be little in civilisation, to which this Theory can be applied. The present-day demand of the female for some recognition of her great value to the race, may possibly be a cry of Nature, a call from out the past.

Human society illustrates the conclusions which were arrived at in Chapter IV by showing that competition does not lead to advancement, which is best gained by environmental differentiation or specialisation.

Finally, it may be said that species rid themselves of males in the following ways :

1. Sacrifice them to enemies.
2. Cause them to destroy one another.
3. Themselves destroy them.
4. Or control their production.