SOME SPECULATIONS ON THE COLORATION OF ANIMALS.

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A short time ago an article appeared in the *Illustrated London News* on the subject of the Camouflage of Aeroplanes. It was stated that "exhaustive experiments have been carried out by experts of all the great air powers to obtain invisibility, and even today, when the camouflage of fixed objects on the ground has reached astonishing perfection, the problem of camouflaging aircraft still leaves much to be desired and causes a wide divergency of views, as may be seen by comparing the British and German schemes."

I submit, with diffidence, that no satisfactory solution of this problem will be found. For the problem is really no new one; life in its flying forms has been faced by it since the carboniferous age and has utterly failed to solve it.

The rest of this essay will be devoted to a consideration of the colouring of wild animals and I hope that, as the subject is a large and obscure one, it will at least serve to provoke further speculation and discussion.

The coloration of animals may be roughly divided into three types: (1) cryptic, (2) conspicuous, and (3) a small group, which includes ourselves and a number of larger animals, in whom the coloration appears to bear no significant relation to the environment. The great majority of wild creatures fall clearly into one of the first two types and are either well disguised or startlingly conspicuous.

Now the principle of cryptic coloration in nature is a well-established fact and the many methods employed and the secrets of their success are relatively well understood. Essays and articles on new aspects of this subject are continually appearing and indeed the phenomen is so universal that it would probably be true to say that if all the wild life of this world stood perfectly still (and kept silent), one would hardly ever see a single creature.

The subject of conspicuous colouring, however, is much less well understood, so it is this aspect of the matter that we shall chiefly study today. I will confine the study to land animals, partly because this essay arose out of some speculations about flight, and partly because a study of the coloration of sea creatures is complicated by the difficulty of appreciating their appearance to each other. (Indeed even the most brilliant colours in these creatures are probably cryptic in effect, such as the blues and greens of those near the surface, and the reds of those in the depths.)

Brilliant and conspicuous colouring in air-breathing animals is seen in a great many birds and adult insects, and in relatively few other creatures, including the Skunk among mammals, some caterpillars, and some poisonous snakes. The vast majority of the possessors of this characteristic are flying creatures, and most notably the lepidoptera among insects, and certain groups of birds.

We will, therefore, proceed to a short analysis of the coloration of birds, butterflies and moths, which has been mainly based on a study of literature dealing with birds in South Africa and lepidoptera in Great Britain and on personal observations of all these creatures in England and Kenya.

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(*a*) BIRDS.

(The following notes refer to South African birds.)

Birds that fly by night and hide by day are cryptically coloured with a spotty mixture of browns, russets, fawns, black and white. A complete list of such birds embraces the Owls, Nightjars and Dikkops.

Birds that spend most of their time on the open ground are cryptically or ruptively coloured, at least so long as they remain on the ground, and exhibit a spotty or patchy mixture of browns, russets, fawns, black and white. A complete list of such birds embraces the Partridges, Guinea-Fowls, Quails, Sand Grouse, Bustards, Coursers, Larks, Pipits, Rock-Jumpers, Plovers and Dikkops. Certain of these birds, such as the Plovers, while extremely well hidden on the ground, are intensely conspicuous in the air. The only exceptions to this rule of the cryptic coloration of essentially terrestrial birds are a few very large ones, namely, the male Ostrich, the Ground Hornbill, and certain Herons, Storks, Ibises and Cranes.

Brilliant and conspicuous colouring in birds is, therefore, confined to those that spend much of their time by day in the air, to certain smaller ground birds when in flight, and to a very few large ground birds at all times.

(*b*) BUTTERFLIES AND MOTHS.

The coloration of these insects appears to be governed by two factors: First, how far the flight is diurnal or nocturnal, and second, the position of the wings at rest.

Now all butterflies are day fliers and when at rest the wings are held vertically backwards in such a way that only the undersides are seen, especially the undersides of the hind wings. Brilliant coloration of the wings is usually confined to the upper surface; and the under surface especially of the hind

wings is almost always cryptically coloured with a spotty or confused mixture of colours.

In regard to moths, the great majority fly only by night, a small number (which includes, in England, the Hawk moths, the Burnet moths, many Bombyces, and the Magpie moth) fly by day especially in twilight. The position at rest varies considerably in the different families, but may be divided for our purposes into two groups: (*a*) those (mainly Geometrae) which spread their wings in such a way that the upper surface of the whole body and of all four wings is visible, and (*b*) those which fold their wings so that only the upper surface of the fore wings and of the head and thorax is visible.

Moths that fly only by night are cryptically coloured with a dingy mixture of browns and greys. The Geometrae are almost always cryptically coloured all over unless (as in the Magpie moth) they fly by day, when they are apt to be brilliantly coloured all over the upper surface of all four wings. In other moths (which at rest show only the upper surface of the fore wings and thorax) the coloration is usually dingily cryptic all over (as in most Noctuae) unless they fly by day (as in the Hawks, Burnets and many Bombyces) when brilliant colours often occur on the upper surfaces of the hind wings and of the abdomen.

In the brilliant coloration of butterflies the whole spectrum is well represented; in that of moths only the lower end is seen, and blues and purples are rare.

Brilliant and conspicuous colouring in lepidoptera is, therefore, practically confined to day-fliers and to those parts of the wings and body that are seen in flight, but hidden at rest.

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Before proceeding to any speculations, let us examine the existing theories that attempt to explain the phenomenon of brilliant colouring in animals.

There are a large number of these theories and at first sight they appear to fall into two groups according to whether the brilliant colours are shared by both sexes, or are a peculiarity of the male. As, however, it is a well-established fact that where brilliant colouring occurs in both sexes of a species it has almost invariably first appeared (in evolutionary history) in the male and only later in the female, it would seem that the distinction is more apparent than real.

So we will not attempt to divide them into groups but will merely take this opportunity to point out that the first six theories are probably true within a very limited field, and the last six are of wider applicability, but doubtful truth.

The theories that appear to be of chief importance are as follows:—

(1) A danger and guiding signal to the herd. This theory may explain the Rabbit's tail, but seems to have little application to the vast majority of brilliantly coloured creatures.

(2) A warning of poisonous or distasteful qualities. This theory appears to explain the possession of brilliancy in a number of noxious creatures, e.g., the Skunk, many poisonous snakes, wasps, the Cinnabar caterpillar, etc., etc., but the great bulk of creatures under discussion are neither poisonous nor distasteful.

(3) The theory of "Batesian" mimicry, where the coloration of harmless creatures closely imitates that of species well-known to be noxious. This theory may explain the coloration of certain butterflies and moths, notably the Hornet Clearwing and the Bee Hawks in England, but again its application is small.

(4) The theory of "Mullerian" mimicry, where many noxious species adopt the same type of "warning" colouring, e.g., numerous species of wasps, the Cinnabar caterpillar, etc., are striped black and yellow.

(5) The theories of associative or terrifying mimicry, where a creature, e.g., the Alligator Bug, resembles some terrifying animal or simply appears strange and frightful as in the case of the Puss Moth caterpillar.

(6) Eye spots (and tails, etc.) on the wings of some lepidoptera may act as attraction marks to their enemies. This is indeed probably a very serviceable device as much evidence has accumulated in recent years that birds often attack these insects on the wing and merely succeed in snatching off pieces of wing. But it is not a complete explanation, e.g., no moth can afford to discard its abdomen, yet it is most common for those with brilliant hind wings to have a brilliant abdomen.

(7) Smith Woodward suggested long ago that excessive ornamentation is to be interpreted as a final flare up of the lamp of life preceeding extinction, that the orderly sequences of growth having fulfilled themselves, the material for further growth is expended in the development of colour and ornament. It might, however, be equally well argued that extinction merely followed in those species in whom the ornamentation happened to become excessive, but we shall refer to this theory again later.

(8) The chief theory that has attempted to explain brilliant colouring where this character is a peculiarity of the male is the theory of sexual selection, originally propounded by Darwin. As it held the field for many years,

and is still apparently regarded as all-sufficient by most we will discuss this theory at some length. By this theory it has been believed that the females of a species generally or invariably selected the most brilliant males, so that the duller-hued were gradually eliminated, and brilliance became more and more extreme. Now this theory (as Pycraft has well shown) assumes an unvarying taste on the part of the females from generation to generation, a taste, moreover, that tends not merely towards brilliance, but towards a particular pattern and arrangement of colours; it assumes an ability on the part of the females to distinguish between the usually excessively slight differences between the males of one generation; and it assumes that such a taste and discrimination not only occur in birds, but in such lowly creatures as insects. These are large assumptions, and the theory utterly fails to explain the fact (referred to above) that when the male has achieved a certain standard of brilliance the female follows.

Pycraft in criticism of this theory states that there is no evidence of sex selection in the development of brilliant colouring. (He can assign no reason for its development, but simply states that there appears to be a trend, or diathesis, that develops late in the history of a species and that progresses with gathering impetus and quite automatically in the direction of increased intensity, concentration and clarification of pigmentation.)

(9) Wallace, in *Tropical Nature,* believed that natural selection could account for secondary sexual dimorphism by supposing that only the strongest and most virile males gained mates, and that these males came to possess an excess of vital energy which became manifest in bright plumes, etc. But what does an excess of vital energy mean? All creatures presumably have a vital energy that is slightly in excess of their normal and average needs and that is kept in reserve for times of stress and emergency, and there is no evidence that the more brilliantly coloured species were more strong and virile.

(10) Bright colours in male birds have been explained as a device for keeping the number of males within proper bounds by rendering them conspicuous to their enemies. But such a device would apply with equal effect to brilliant females, of which there are many, and the whole species in this case would be kept within "proper bounds," which is ridiculous.

(11) Fisher, in *Watching Birds,* says: "It is highly probable that the bright colours and adornments of certain male birds have as their primary biological purpose intimidation and threat rather than attraction. This applies

to birds which have bright plumage only in the male (like pheasants and some buntings), only in the female (like phalaropes), in both sexes all the year round (like robins and jays), or in both sexes in the breeding season (like black-headed gulls)." This theory is closely bound up with the theory of bird territory defined by Lack as an "isolated area defended by one individual of a species or by a breeding pair against intruders of the same species and in which the owner of the territory makes itself conspicuous." As such, the intimidation theory, therefore, has no application to butterflies and moths.

(12) It has been shown that certain birds recognise other members of the same species and distinguish their sex by observation of colour pattern. Very likely this factor plays a part in the recognition by individual creatures of their fellows throughout a large part of the animal world. But we have no reason to believe that conspicuous colouring is necessary for this purpose: the vast majority of animal life manages just as well without it.

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These are the existing theories, and it would seem that they fail to explain a large part of brilliant and conspicuous colouring in animal life; that they may explain the phenomenon in most creatures that creep, crawl and walk and a few that fly; that the phenomenon occurs most commonly in flying creatures, and that the problem as it affects these has been inadequately answered. (The explanation might, of course, be different in different types of flying creatures, but we feel that the facts warrant the assumption that in general it is the same, as we will endeavour to show.)

I submit first that certain creatures by reason of their size or of their habits of life are necessarily conspicuous, and that if this is true, any type of coloration is from the point of view of producing invisibility, equally valueless. That under these circumstances brilliant colouring often develops and under no other circumstances, except for the few examples (snakes, caterpillars, etc.), that can be explained by existing theories.

Now at least 99% of camouflage consists in keeping still and indeed the great majority of cryptically coloured creatures behave as though well aware of this. But one cannot keep still in the air, so that creatures that fly cannot hope to conceal themselves from their enemies while in flight. It is probable that if the sea were always blue all sea birds would be coloured blue on top; and that if birds migrated by following closely one line of a railway track, they would develop a black stripe down the middle of the back. But in fact the sea is not always blue and birds do not migrate that way, and the aspect of the

earth varies notably from moment to moment as one passes over it. Camouflage in the air is useless, and birds that spend much of their time in this element, and butterflies and moths when in flight, are released from the need to employ cryptic colouring.

A certain number of larger mammals and large terrestial birds are necessarily conspicuous on account of their size and habits. The large birds previously mentioned as exceptions to the rule of the cryptic coloration of predominantly ground birds are all waders in open shallow water or stalkers in the open veldt and as such are necessarily conspicuous. Moreover, it is well. known that many big game hunters deny that camouflage occurs in the larger wild mammals. Camouflage is useless in such creatures and they are released from the need to employ it.

Now this theory raises a further question. If a species, by reason of its size or habits, is released from the need to employ cryptic colouring, one might expect that its coloration would develop in a purely haphazard way. Does it in fact do so? The answer seems to be: in domestic animals, usually; in wild animals, never.

Domestic animals are not subject to the ordinary laws of evolutionary survival and often exhibit colours that are not only grossly different in individuals, but are often asymmetrical in the same individual. The question, however, as it affects domestic animals is too complicated to be discussed in this article.

Wild animals rarely exhibit gross differences of colour as between individuals of the same species, and hardly ever exhibit asymmetery. Their colouring does not develop haphazardly and brilliant colour when it occurs progresses (as Pycraft says) in the direction of increased intensity and clarification of pigmention. This type of coloration, therefore, appears to have some positive value, so we are led to ask the further question as to what this value is.

I submit secondly that brilliant colouring when it occurs in flying creatures is meant to be seen, or, to put this in a more scientific way, that it has a value which is related to the world of vision. This might appear rather obvious at first sight, but in fact many conspicuous colours are in no way related to the world of vision, e.g., the bright-green of most leaves and the black of a negro's skin have a purely physiological value.

Now what evidence supports the theory that brilliant colouring in flying creatures is meant to be seen?

Such colouring never occurs in purely night-flying creatures such as owls, night-jars, bats and purely nocturnal moths; and it does not occur in parts of the surface of the body that are never seen (e.g., the part of the hind-wing that is overlapped

by the fore-wing in lepidoptera), but always in parts that are visible in flight. Moreover, it seems most likely that the fact that such brilliant colouring as occurs in twilight-flying moths is confined to reds, oranges and yellows is due to the emphasis laid on the lower end of the spectrum by evening light. Such light, as compared with broad daylight, contains relatively few blue rays and many red. The colours are meant to be seen.

But why? Has brilliant colouring some positive protective value to its possessors when in flight? (One can imagine, for instance, that it might produce a flickering flight that was difficult for enemies to follow.) If, however, brilliant colouring had a positive protective value in the air one would expect to find it as universal in flying creatures as cryptic colouring is in terrestrial, but this is by no means so, as many birds and butterflies are dull at all times. One would expect to find it as well-marked in the females as the males, for the former are individually more essential to the survival of a species than the latter. One would expect to find it best marked in those birds, butterflies and moths that were most subject to attack and least marked in those that were comparatively free from attack. Now J. C. Mottram, in an article on the Secondary Sexual Characters of Birds, has classified birds in various ways in relation to their freedom from or liability to attack, and points out that oceanic, maritime, and aquatic birds are probably the least liable to attack. Yet such birds are almost invariably most conspicuously coloured in black (or very dark-brown) and white. Finally, such a theory of flickering flight does not touch the question of the brilliant colouring of the larger ground birds.

It would appear, therefore, that in brilliant colouring in flying creatures we see a quality that has no protective value, and apparently no survival value.

The quality appears to have arisen (like all other natural qualities) as an evolutionary experiment; it has arisen as a by-product of the pre-existing pigmentation of feathers and scales; and it has been perpetuated simply because it has been untrammelled by the ordinary laws of evolutionary survival. The reason for its steady enhancement in many species, on the lines described by Pycraft, remains obscure. But I submit that the fact that this steady enhancement occurs (quite independently of natural or sexual selection) is a strong argument in favour of certain aspects of the discredited orthogenetic theory of evolution.

By this theory the germ-plasm is assumed to contain a faculty that makes it tend to vary always in one direction from generation to generation. It would seem that this faculty does exist, but that it is usually modifiable and is only rarely allowed full play by a competitive environment. It is, moreover, quite

possible that if this faculty is allowed full play for too long it may become not merely irreversible (as has been demonstrated to have occurred in certain static biological characters, such as some elements of the reptilian skeleton), but, in a dynamic quality such as this, unarrestable. There is, of course, a limit to brilliancy of colouring, but in the case of other types of ornamentation such a state of affairs might well lead to extinction. The theory would thus explain Smith Woodward's observation, based mainly on a study of fossil reptiles and the bizarre forms of many of these, that excessive ornamentation is apt to precede extinction.

If we admit this explanation of the development of brilliancy it is surely not surprising that the quality occurs first in the male. For he, individually, is less essential to the survival of the species, and evolutionary experiments are less dangerous if they occur first in him. If he can get away with them the female follows on the same lines, unless her manner of life is so different as to debar this.

Before closing this essay it might not be irrelevant to point out that, if this explanation is correct, brilliant colouring has followed lines of development that are not unique in the world of today. One can think of several other biological qualities and faculties that appear to have been free to develop untrammelled by the ordinary laws of evolutionary survival, e.g., the song of birds, the play of birds and mammals, and many of the higher faculties of the human mind. And it is of interest to note that all such qualities, when released in this way, seem to develop on lines that can only be described as aesthetic.

To take one example among many, one might say that abstract thinking has simply arisen as a by-product of utilitarian thinking and that it has been perpetuated because the quality has been untrammelled by the ordinary laws of evolutionary survival. It is at present mainly a characteristic of the male, but, as an experiment, its success in this year of grace 1941 seems so slight that it is even doubtful whether the female will ever have a chance to follow.

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Which reminds us that the camouflage of aeroplanes is probably useless.

REFERENCES.

Collenette, C. L., 1935. "Notes Concerning Attacks by British Birds on Butterflies." Proc. Zool. Soc., London, **2**, 201—17.

Fisher, J., 1940. Watching Birds, London.

Mottram, J. C., 1915. "Some Observations on Pattern-Blending." Proc. Zool. Soc., London, **4**, 679—92.

Mottram, J. C., 1915. "The Distribution of Secondary Sexual Characters Amongst Birds." *ibid,* **4,** 663—78.

Noposa, 1923. "Reversible and Irreversible Evolution." Proc. Zool. Soc., London, **4,** 1045—59.

Parker, T. J., and Haswell, W. A., 1928. Text-book of Zoology, London.

Pycraft, W. P. Various articles in the *Illustrated London News,* 1936-1941.

Roberts, A., 1940. The Birds of South Africa, London.

Stewart, A. M., 1913. Common British Moths, London.

Wells, H. G., Huxley, J., and Wells, G. P., 1931. The Science of Life, London.