

XXVI. *Protective Coloration in its relation to Mimicry, Common Warning Colours, and Sexual Selection.*
 By ABBOTT H. THAYER. Communicated by
 PROF. EDWARD B. POULTON, M.A., D.Sc., F.R.S.

[Read October 21st, 1903.]

THE following paper records an artist's examination of the principles of butterflies' coloration, and shows how the results tend to restrict the fields heretofore claimed for Mimicry and Common Warning Colours, and to place them on a basis of Concealing Coloration. It contains also several arguments tending to restrict the hypothesis of Sexual Selection.

It does not attack the obvious fact that every possible form of advantageous adaptation must somewhere exist. It is obvious to its writer that there must be unpalatability accompanied by Warning Coloration,—as apparently in the cases of the Hornbills and Wood Hoopoes reported by Mr. Frank Finn, and probably in many Corvidæ, for instance,—and equally plain that there must be Mimicry, both Batesian and Müllerian. Yet every case demands special examination, for the reasons that I shall show herein; and no apparent conspicuousness of coloration is sure to prove such when examined on the principles established in this article.

First, it seems necessary to establish the artist's claim to be *the* judge of all matters of visibility, and the effect, upon the mind, of all patterns, designs, and colours. If even the artist is limited in this, his own field, what hope is there for others? Fullest wisdom on the part of naturalists would make them adjourn all matters of animals' appearance to us artists, just as any wise ruler gathers about him the most highly specialized minds, to widen, through them, his own scope.

An artist reads design wherever it occurs, just as a composer reads a score, without playing it, or hearing it. He perceives that every juxtaposition of spots, or shapes, or colours, or of dark and light, and of degrees of these,

is just so much representation of some structure, whether the representation be accidental or intentional. He sees at a glance in marble-veins, the grain of wood, etc., not *imaginary*, but *actual* representations of natural objects and perspectives, and weighs the correctness of these. Nature has evolved actual Art on the bodies of animals, and only an artist can read it. When he examines the colour and colour-pattern of the animal kingdom, he sees that zoologists are hopelessly off the track in their general conception as to which coloration is to be called conspicuous, *i. e.* rendering its wearer so. *Any* coloration or pattern would be conspicuous *somewhere*, and Nature cannot prevent animals from straying beyond the environments that would most perfectly harmonize with their colour and pattern. But let us take the broadest possible survey, and we cannot doubt that most animals wear on their coats pictures of their habitat. As I before pointed out, even the under-sides of the wings and tails of hawks bear the general twig-patterns so common on forest birds, as if Nature found it worth while to efface the white silhouette their wings' under-sides would make when they extended them while perching. We see how completely such patterns (when couched, of course, as they always are, in the effactive gradation) *do* help to obliterate a partridge, grouse, woodcock, hare, or any other of almost all the species in every order; since they prove to be actual *animated pictures* of their environment. As I said before, in my paper on so-called "Banner-marks," * these forest-like patterns are found on forest creatures, and not on desert creatures, or ocean creatures. Sand-birds are usually marked in longitudinal, delicate patterns, very like those the sand assumes when seen at the same angle at which one observes the birds themselves. Tigers and zebras are resolved into pictures of tall, strong flags, grasses, and bamboos, while the lion is a picture of the desert. (It will some day be plainly understood that the effactive gradation is the essence of the success of these patterns. Were they not arranged to compose one perfect counter-gradation, from top-dark to under-white, they would appear merely as what artists call "lines of quantity," like the hoops of a barrel, *emphasizing* the rotundity, not effacing it.)

Now, let me prove that *any* pattern would somewhere be

* 'The Auk,' vol. xvii, 1900, p. 108.

conspicuous. I once saw a skunk (*Mephitis americanus*) crossing a snow-field near at hand. This animal is black (with the slight amount of efface gradation found even in black animals), with a large white pattern on top. He was totally unrecognizable, because his white against the snow was undistinguishable. His black was left to form a most grotesque silhouette. Had he been against black, it would have been this black part that disappeared, and one would have seen only an unrecognizable, moving *white* thing. Naturalists' lack of understanding this principle's immense import has gone far to strengthen the present Mimicry and Warning-Colour theories, which may prove to have been evolved, largely, in the effort to explain supposed conspicuousness, where such did not exist. A tiger in the desert sands, though his gradation would still, more or less, efface his solidity, would nevertheless show his *pattern*. His bamboo-vistas would be plainly a failure against the sand. The lion in the bamboos would, when not covered by them, tend to present an unaccountable *flat silhouette*,—a lion-shaped section of desert-landscape, out of place. On the same principle, a white patch on striped cloth or a striped patch on white cloth would be conspicuous. We see on all hands evidence that Nature cannot help moving forward to the utmost completeness of protective devices;—that, in fact, she cannot grope or blunder. A marvellous, turquoise, emerald-green and red-coral-marked Mediterranean fish looks conspicuous on the fishmonger's slab; but follow him to the sun-lit ocean grottos which he inhabits, and of which he is a wonderful picture! No, the whole use of the word *conspicuous* is mainly born of the zoologist's lacking the artist's sight.

Let us now turn to the field in which the naturalists are most conspicuously at fault, that of the butterflies and moths. One glance of an artist,—that is, of an artist accustomed to lifelong looking at vegetation and butterfly-life,—at a world's collection of butterflies, shows him that they are mainly either flying pictures of various combinations of flowers and their backgrounds, pictures of the *shadow under foliage*, with delicate patterns of vegetation or flowers drawn across it, as, for instance, in the North American *Papilo polydamas*, and the dark *Satyrinæ*,—or that they are wonderful representations of flowers themselves, as in the *Pierinæ* (all but their usually narrow dark

border), many of which even bear a representation of six stamens (counting their two antennæ), and, what is very common in butterflies, a wonderfully perfect shading on that part of the wings next the body, grading toward it in a way that makes it appear like the bottom of a concavity. My photographs of *Limenitis* (*Basilarchia*) *arthemis* show the flower-form, the appearance of the rim of its cup being carried across the butterfly, as in the species of *Precis* which wear a large, bright semicircular bar, cutting them as the skunk's white cuts him.

I should have placed at the beginning this axiom: *Only unshiny, bright monochrome is intrinsically a revealing coloration.* As soon as patterns begin, obliteration of the wearer begins, as shown in the case of the skunk. Nature does not blunder, and Natural Selection would evolve the monochrome, instead of a patterned surface, were simple conspicuousness her aim. Also, she would, if she used patterns mainly as badges for identification of the wearer, have omitted the delicate subtleties that go to make up the patterns of most butterflies. Let us apply the skunk-lesson to the many dark butterflies which wear more or less bright, clean-cut patterns. As they rest on flowers, their *dark* matches very closely the shadow-depths *between* the flowers, especially when seen from above or outside the flower-mass; and, in fact, the delicate general gradation and *faint* detail existing even in these parts, appear to an artist to represent the near vistas under the flowers; while the bright pattern is likely to echo the notes of the flowers themselves. Only artists understand this colour-echoing. The artist's sight is conscious, as it ranges over a scene, of every recurrence of each colour-note. This colour-note, wherever seen, seeks, as it were, *its own*, in his brain,—just as a violin-string rings when its note is sung. In a book we are writing on protective coloration, my son and I shall show larvæ that resemble *things* (already well known), larvæ that disappear, larvæ that appear to be extensions of leaves; and larvæ with many other startling and dissimilar concealment-schemes. What wonder if in butterflies there prove to be as many different forms of concealment? It is impossible to lay too much stress on the fact that all patterns which look so striking and bizarre, when *off* duty, are, when *on* duty, up to the moment of detection, precisely the workers of the magical illusion that conceals. It is inconceivable that birds should

more easily recognize minute patterns than colour, when we realize that the perfect colour-adaptation of innumerable forms of life, from mammals to larvæ, proves *that the lower animals see colour* (since otherwise such adaptation would not be necessary for their concealment). In each form of protective coloration there exist cases so pronounced as to leave no doubt of their use. Each of these has been assumed to be mimicked, or, at least, echoed, for some reason, by other species than the one in which it is most perfect. Let us look at the dead-leaf pattern, *i.e.* the pattern that represents, in the most minute degree, substance of the *colour and thickness of dead leaves*, and lying as near the ground as dead leaves usually lie. This pattern is marvellously perfect on the Copperhead snake (*Trigonocephalus contortrix*), on some Boas, on that form of domestic cat which has the most tiger-cat-like black and grey pattern (as well as, in fact, on tiger-cats themselves), and on several Sphinx moths. Of course, when this leaf-representation occurs on the rotundity of animals' bodies, as in the cats or snakes, it exists only in co-operation with the regular effactive gradation, but on the flat plane of a Sphinx's upper-wing-surface it has and needs no such co-operation. In the Sphinx-moth photograph which I have sent Professor Poulton, this reproduction of thin material casting a shadow on the surface it lies on is past all mistaking. This artifice is present on many moths, and its elements are traceable in such butterfly genera as *Vanessa*, *Grapta*, and many others. To know at what point in the long series of somewhat similarly marked species the original function has ceased, would require impossible study.

While it is plain that a hundred needs may each be represented in the pattern- and colour-schemes of animals, it is also plain to an artist's eye that in most butterflies all visible details of colour, pattern, and form are essential parts of the representation of flower-scenery. And it is surely conceivable that, in a certain region, one particular form of flower-scenery-representation may furnish such advantages to butterflies as to cause many widely-separated species to become modified till they wear a common aspect; and it is conceivable also that there would be one common form of wing which would best lend itself to this scheme. Surely we do not know enough of the habits of these insects or of the regions that may be their strongholds to

feel sure that this hypothesis is absurd; and were it correct, it would complete a chain of seemingly perfect evidence.

After we see how inexplicable it would be if butterflies did *not* either resemble flowers, or represent some portion of flower-scenery, why should we, in view of the endless variety of flower-forms, stick at any form or pattern in the butterfly that frequents them? One must constantly remember that *any* pattern is less conspicuous than bright, unshiny monochrome. Therefore, "*conspicuous*" is not the right word for the character of patterned butterflies.

Now since the *Ithomiinæ*, *Heliconinæ*, and *Danainæ*, such for instance as the similarly coloured cow-red and chrome-yellow, black-bordered *Melinæa*, *Heliconius*, and *Lycorea* (and equally, in other colour-schemes, all the other so-called mimicking groups), are in every way completely painted by Nature into these three tones,—the note of *shadow under vegetation* making their borders, which it occupies, coalesce with the shadow under the flowers, and disappear, while the red and chrome wonderfully reproduce the colours and patterns of such flowers as *Odontoglossum triumphans*, who shall say that it is not to this flower—which perhaps, by its abundance, dominates the region—that these cow-red and chrome-yellow butterflies owe their common appearance? Some such flower may be overwhelmingly attractive for its honey.

Perhaps the most conclusive of all our evidence is to be seen in the transparent winged members of these mimicry groups. *Dismorphia orise*, for instance, with its green transparencies enclosed in a pattern of the same velvety dark fuscous that I have already described. What conceivable artifice could offer greater opportunity for frequently remaining unnoticed amidst flowers and leaves?

These little green windows must of course allow any bright object to show through them, while the fuscous cuts the aspect to pieces by representing a shadow far below the insect. The very word *transparent* wrecks any theory of conspicuousness or adaptation suitable for a badge. Add to this the present belief that the transparency has been attained through selection, and ought not those who hold this theory to believe that concealment was obviously the goal of a *change toward invisibility*? It is hard to conceive of a better device for representing little green leaves than by these glossy green, leaf-shaped,

and leaf-veined windows, bordered with imitation background, and ever ready to look like glossy leaves the moment they are extended over a bright flower or other bright object.

Professor Poulton has already noticed the efficacy of the imitation hole in the wing of *Grapta* (a device similar in effect to the gold dots on some pupæ).

During the writing of this article I have been learning that iridescence itself is an immense factor of concealment, far greater than I at first realized. I have lately had excellent opportunity to study several species of golden-brown butterflies with sheeny black tips spotted with white, and I begin to realize the wonderful power of this combination. The white dots *stand changeless*, while upon the black, in bright sunlight, faint rainbow sequences dissolve the *actually* flat wing-surface into liquid depths, apparently wholly detached both from the insect and from the white spots, which appear, as I before said, to be shiny points like dewdrops down in the spaces below the butterfly.

If butterflies were mimicking each other, Mr. Blandford's objection (Proceedings of the Entomological Society, 1897) that the resemblances would be hypertelic would seem true. Since an attempt on Nature's part to give common colours and patterns to a group of insects involves no need that any one of them shall have sharp delicate contours of spots, or have subtle gradations, these species would, if their object were to resemble each other in their colour and markings, stop short of such sharp contours, etc. On the other hand, if they are representing flowers or any organic *forms* instead of merely patterns, etc., *on* forms, they would profit by the utmost minute finish of every part of their design, since just this *finish*, this microscopically perfect smoothness and minuteness of detail is an essential characteristic of flowers and even of leaves.

Upon my hypothesis, the many "warning-colour" species that have dull-contoured spots instead of sharp ones, would seem (as they do to the supporters of Mimicry) to be species in process of adaptation, but *to the aspect of flowers*, instead of to that of each other.

As soon as the advocate of the Mimicry theories sees that to wear the region's prevailing pattern *tends to conceal*, his case looks bad; since we see throughout the animal kingdom common coloration, and often common

form in widely separated orders, plainly accompanying common environment and habits. The Salmon's silver, grading upward into dusky, and downward to purest white, is identical with that of countless fish in many groups, and no one doubts that environment and habits are the cause. Among birds, *Emberiza miliaria*, *Anthus pratensis*, *Alauda arvensis*, and *Alauda arborca* are four species of three genera for all four of which *one* minutest colour-and-pattern-description would almost suffice; and the same colour-scheme and pattern with slight variations is found on a great many other species throughout the world, both of *Passeres* and even *Scolopacidæ* and *Gallinæ*, telling plainly of *life on the ground amidst grasses*. Among the *Scolopacidæ*, many females and young of the *Anatidæ*, and the *Laridæ*, Nature betrays, in the main, great lack of variety in design, easily accounted for by the lack of variety in the aspect of the environment. In a broad survey of the animal kingdom we perceive that everywhere the degree of colour-and-pattern difference between different members of an order, family, or genus keeps pace with the degree of variation in their environment's aspect.

Why may not the circumstances of a group of butterflies furnish them similar needs to wear a common livery, even if we cannot see the reason? Might they not tend also to have their *flavour* similarly affected by similar food? The Spruce Grouse (*Canachites canadensis*) is saturated with spruce flavour, and the world is full of such cases. Even the amazing similarity between members of these groups is no proof they may not, for reasons which we have not discovered, profit each by exactly the same form of concealing-coloration. It should be borne in mind that it is not a *flower* that these mimics evidently represent, but a certain combination of the flower's aspect with that of its surroundings. Hence there may be one best way to render this. Butterflies on wing are conspicuous, but are wonderfully protected by their jerky flight, which is completed by their wings being so large as necessarily to throw the body up and down at every movement. This latter advantage, attainable by no other conceivable means, may be a great factor in the whole matter. In flight they are doubtless practically safe, *i. e.* too troublesome a quarry to be seriously decimated. I send, for Professor Poulton to exhibit, photographs of a number

of so-called conspicuous butterflies (dead specimens), the examples having been placed as far as possible without an unfair attempt to favour my argument, except in a few cases where the attempt is obvious. Surely they speak eloquently. Could they be seen in their colour-coalition, they would speak even more so. Any one *carefully* examining them will see that, in most cases, their dark parts are not distinguishable from the background (*although the average person, unaccustomed to analyze his sight, will, by recognizing the butterfly through its pattern, fancy he sees every part*).

The very keynote of the zoologist's error is psychological. One *sees* only what is out of place ;—that which is *in place* is harmonious and unnoticed. We know how many of these concealed animals we *see*, but we do not dream of how many we *pass by*.

By tracing back to so palpable an example as our Sphinx-moth photograph, we see that the various combinations of sharp-edged markings with delicate blendings, exactly resembling the combination of patterns made by any sharp-edged fabric lying near a ground on which its shadow falls, do *represent* such combinations of form ; so that we must believe that so elaborate and delicately complete a design would scarcely exist merely to identify a species as unpalatable. We find on several *Preces*, as on many *Vanessæ*, and *Papiliones*, very highly developed cases of the varied combinations of design worn by multitudes of the most obviously protected birds, and other animals ;—slight variations of representation either of near objects casting a shadow on the background, as in the cats, snakes, and moths mentioned, or of near objects relieved against more distant, fainter ones, as in the European Woodcock's wings, many female Pheasants, and male Pheasants' tails, such as that of the Copper Pheasant. Doubtless each species has some particular headquarters, as it were,—some region which it fits best,—and unless we chance to study it in this very region, and at the most favourable season, we shall never witness the full operation of its protective colour-scheme. Mr. Frank M. Chapman has already pointed this out in a paper entitled "On the Birds of the island of Trinidad," published Feb. 1894, in the "Bulletin of the American Museum of Natural History," a paper containing some very prophetic glances into the future of protective coloration.

Apparently Nature has two main protective-colour schemes; one of which is closely imitative of the *very near environment* of the animal, and applicable to such species as sit close, and keep still, for concealment, as do the tree-toads, moths, goatsuckers, certain snakes, and, among butterflies, the species of *Grapta*. (The latter, at least, keep very still when resting, and expose at such times only the rock or bark representation on the under-side of their wings.) Among those butterflies, on the other hand, which have no pronounced habit of protecting themselves in this manner, Nature seems to have been forced to a bolder, more positive way by furnishing them an upper-side bearing a sort of conventionalized representation of the predominant details among which they are destined to move. Flowers, of course, must almost always be present. And always the notes of the conventionalization are *perfect*. Here is a most impressive argument, viz., so-called conspicuous butterflies have the body, head and all, exquisitely effacively graded. Would it not be absurd for Nature to spend energy in *effacing* the *body* while making the *wings* *conspicuous*? The multitude of species, the world over, whose main colour is largely the peculiar fuscous of shadow under vegetation, have in most cases not merely this shadow-colour, which so perfectly coalesces with the shadow and apparently vanishes from the insect, but also a system of exquisitely delicate perspectives *within* the patches of shadow-colour; as in the genus *Caligo* especially. I mean that *Caligo* is an exquisitely developed representation of the perspectives which an artist sees in peering down through the openings between the flowers. The parts of the world which I know well do not yet furnish me a clear vision why so many butterflies, such as several *Preces*, and *Anosia plexippus*, for instance, have these delicate perspectives done in golden brown instead of either shadow-colour or the more delicate flower-colour; but that this delicate design does represent perspective, and would be wasted if used for any attempt at conspicuousness, and that it is entirely akin to the perspectives rendered on perfect shadow-colour in so vast a number of species, is reason enough for trusting it to prove to be some form of concealment device; and on red flowers these species show surprisingly little. I myself suspect that butterflies of the *A. plexippus* type represent half a concave flower. Watch any butterfly of this class, or any

of the classes in which the pattern, when the wings are open, arranges itself in amphitheatre-like semicircles of stripes or dots, etc. When such a butterfly rests with open wings on a flower, its head is at the centre, its antennæ form two stamens, and these semicircles seem to belong to half the flower of which its head is the centre. In several *Preces*, and many other butterflies, there is a general representation of something like a bunch of stamens casting their shadow deep under them in the flower's cavity. Usually a butterfly's upper-side has the exact colour-note characteristic of flowers and flower-scenery seen from right overhead (take, for example, *Papilio turnus*); while its under-side is a picture of such greater distance as would be seen from the *side* position necessary for beholding it when the wings are in their characteristic vertically-folded position; and this is the position from which enemies on neighbouring bushes would see it. So-called "conspicuous" butterflies have, in short, their upper-side designed with the full strength "values" of the nearest flowers looked into from above, and their under surfaces designed in notes more delicate, to counterfeit the distance, and a perfectly effactively-graded body. Their under-side is also more delicately finished, as if against the nearer inspection possible from neighbouring bushes. In fact, they wear every conceivable aspect to fit them into the background from each point of view, and make you think you see through them; or else, seen from above, to make you think, as in the case of the *Pierinæ*, that you see a flower itself. How can such a case call for a theory that is based on the hypothesis that they are conspicuous? One very important fact is that we have abundant proof that animals, including birds, have totally different sight from ours; and the existence of these patterns, etc., unless it can be denied that they even *tend* to efface, should be taken as proof that they sufficiently *succeed in effacing*. Otherwise, why are they there, when almost the whole animal kingdom does need concealment? A fox, a deer, a bear, a grouse, a turkey, or any small bird or mammal, may come almost to one's feet if one stay still, yet flee wildly on seeing any motion. Is not this sufficient proof that even if we were usually able to detect a *Papilio* when it is effactively situated, it is no sign that a *bird* could do so, if the insect kept its place?

Butterflies very often remain unobserved amidst flowers or other vegetation, by any one approaching (especially if he be not keenly in search of them) until once flushed. Of course our yellow and our white *Pierinæ* are pretty sure to catch the eye of the person approaching, if, as very commonly, they are found amidst dark vegetation. Yet their colours are precisely those of our most abundant flowers, just as they are our most abundant butterflies. This fact harmonizes with my argument that, however conspicuous in many situations, few animals are so in the place or region to which they doubtless owe their abundance. We see largely the overflow individuals *from* a concealing region *into* a less favouring one, and erroneously think of the species as typical of the region where it is visible to us. The gentle waving of the wings, so common among butterflies when they are feeding, seems plainly a protective imitation of the swaying of leaves and flowers in the breeze. Any one who has photographed outdoor vegetation knows how seldom it stands still.

To sum up, the general aspect of each animal's environment, throughout the animal kingdom, is found painted upon his coat, in such a way as to minimize his visibility, by making the beholder think he sees *through* him. How has it chanced that, while this fact has long been recognized, in a crude way, in many fields of zoology, it has remained essentially unnoticed in butterflies? Their most critical moments being passed upon flowers, the aspect of flowers combined in various proportions with the dark vistas down among them to the shadowy earth beneath, is exquisitely painted upon a vast majority of the world's butterflies, and on none more plainly than on those called conspicuous. The *Pierinæ* are mainly representations of flowers, though surrounded by a dark border which appears to belong to the shadows beneath it. On the other hand, there are a vast number of dark species which represent a portion of this shadow-under-vegetation, with bits of yellow vegetation, or of flowers, seen against it (these of course being rendered by the light markings). Could small, bright patterns on dark possibly be more perfect generalizations of small blossoms, buds, and stems?

I cite the following examples of the various colorations described.

Among the *Brassolinæ*, *Caligo eurylochus* is a marvel of

wholly efface design, so subtle as to make it absurd to suppose that Nature could be trying to have him conspicuous, or to use such delicate gradations for *identification*. *Caligo telamonius* and *Caligo demosthenes* are even more wonderful examples. *Cynthia* has a wonderful multiplicity of perspectives represented on its surface. Black and green *Nymphalinx* are notably orchid-like in design. Their dark tips disappear, uniting with the shadows. *Dione* has good near-scenery on its upper-side, while the silver spots of its under-side appear in a side view to cut holes through its wings.

The Danaine butterfly *Limnas chrysippus* is covered with design which I am not prepared to interpret. Whether or not it is a flower, the four interior spots on the upper-side of the hind-wings may pass for stamens, as may also, of course, the antennæ; and whether or not the yellow-red ground counterfeits the colour of a flower, it represents a flower's form. *Caduga melaneus* has the colour-scheme of the skunk, with, of course, similar advantages.

The *Satyrinæ*, i.e. the dark ones, with strong, light patterns, have also the skunk's colour-principle. The *Danainæ*, *Ithomiinæ*, and *Heliconinæ* of South America, *Lycorea*, *Melinæa*, and *Heliconius*, for instance, display marvellous mutual resemblance, yet their likeness to *Odontoglossum triumphans*, when their dark tips are cut out by coalescing with the shadow, is most impressive.

Among the transparent *Satyrinæ* I may mention *Pierella nereis*. Unmistakably the whole surface of this insect (and likewise that of *Cithærias menander*) pictures a single flower.

Pierella astyoche represents flower-scenery (likewise *Pierella rhea*).

In the Oriental Danaine genus *Euplœa* we see exquisite shadow-perspective over which white spots relieve. The blue sheen, seldom or never occurring on both wings at once, additionally effaces.

In the *Lycænidæ* the exquisite *blue* species represent flower-cups, their black border of course detaching into the background.

The above examples I have chosen from all the families I have lately examined, which do not include the Skippers, or the great mass of *Papilionidæ*.

Let me add a few more reflections, all harmonious with my theory.

The act of flight tends to obliterate pattern, by the too quick substitution of one colour for another before the eye. A black-and-white butterfly, therefore, tends to look simply *grey* in flight.

It is not necessary to conceive that a bird must find the imitation flower on its proper plant, if the flower represent a type common in the neighbourhood. A vast majority of butterflies, including most members of Mimicry groups, have the common dark wing-tips of the *fuscous* colour which causes this portion to seem lacking from the butterfly, leaving the lighter-coloured parts to represent a more flower-like form. The white dots, so common on these black tips, surprisingly aid the representation of *space below the flower* by supplying the average sharp details that are to be seen down in the shady under-spaces,—little glints of light on twigs, etc.,—and their dark ground is rendered additionally transparent in appearance by iridescence.

If the foregoing arguments prove that the so-called Warning-colours commonly cited do not exist mainly to make their wearer conspicuous, it does not follow that they may not still serve *secondarily* as Warning-colours. When, for instance, they happen to fail to conceal, they may then serve to warn. My main point is that they first of all *conceal*. I suspect that the same principles apply to striped wasps and hornets, and many other insects called conspicuous. The yellow pattern unmistakably allies their appearance to the pollen-covered flower-interiors, making them far less conspicuous than an unmixed need to be seen would have them. Yet when seen, they may well profit by the pattern's recognizability.

Can any one, once shown, as I here show, that butterflies' patterns are *not* intrinsically the thing to make the wearer conspicuous, and shown that they *are* wonderful representations of the flower-scenery I describe, believe that Natural Selection has bungled, and *wasted* design of the most intricate kind? No, it is the beauty of the whole thing that *absolute fitness* is the goal of all changes by Natural Selection:—is, in fact, the only motive-power; changing all forms steadily toward itself.

We see, then, that butterflies are imitation flowers, or pictures of flower and background. This has escaped the eye of zoologists. They see that fish wear representations of under-water scenery; that forest animals are forest-

patterned; beach animals, beach-patterned, etc., through the whole animal kingdom. But this other obvious case has escaped them. What other equal hope were there for insects that feed in full sunlight on masses of bright flowers?

In another paper I shall extend this criticism on the animal-conspicuousness-theory to the field of birds, and to strengthen the present paper by showing reasons to suspect that this theory is also not well intrenched in the bird part of its field, I append the following examples of the material to be used in the next paper.

Several of the most apparently conspicuous details of the exteriors of male birds can be shown to be such as would aid them to escape their enemies, and it is plain that simple life-preservation must for ever take precedence in the scale of importance of animals' needs. It is a mild statement to say that if the animal kingdom is to survive, females have greater need of the mere *existence* of mates than of any particular attribute in them, and if this statement is true, in all its immense import, it is among the most primitive needs of the male, that we should search for the explanation of his present attributes. All the nuptial developments, either of feathers or fleshy growths on beaks, etc., are much more rationally explicable along the simple lines of utility, than those of direct Sexual Selection, since it is apparent that every appendage, and every brilliancy of colour or costume adds to the formidableness of a warrior's aspect. One male conquers another partly through overawing him by superior splendour, and actually looking larger by means of his appendages, and when these gaudy-feathered braves flaunt before their females, why are they not presumably appealing to the females' love of a good fighter,—a sentiment so dominant, even in the human race,—and a simple sense of what constitutes a husband full-equipped for the rough work devolving on all feudal lords? In fact, from which end of the animal scale is this human sentiment traceable? If from the lower, as seems obvious, it must exist there. I believe that a material need for any existing thing will always be found to precede the spiritual, just as simply as a man must *catch* before he can *eat*, and will *then think*.

These arguments suggest, at least, that the nuptial superficial developments are for the direct use of the male who wears them. Let us look at the iridescent splendours

of the Peacock family. An artist can see that whereas unshiny monochrome reveals its wearer to the utmost, iridescence, on the other hand, destroys visibility of surface, by substituting for a normal light-and-shade gradation, a totally new succession of colour and light notes, and above all one that changes its character with every movement of the bird, and every change of the beholder's standpoint. Add to this in the Peacock's case, for instance, his habitual resort to dense cover, and his gorgeous blue and green gleams, through its interstices, present merely the aspect of foliage-colours and hints of flower-masses. I feel sure that Peacock hunters will testify that this bird is hard to see when lying close.

Let us imagine an animal stalking this bird. He will look *wholly for motion*:—(such at least is the habit of all predatory creatures I know). Now it is the peculiar property of sheen, that it will *stand still* while the thing it is on *moves*. This means that a Peacock can move his brilliant neck, while its sheen *stands still*,—just as the gleam on the telegraph wires keeps pace with the railway train as one sees it from the window. And since this gleam of the bird's neck must be the most visible thing, the possibility of the neck's gliding along *behind* it, while *it stands still*, must often save the Peacock; (for the balance between the *evolved skill of the hunter* and the *evolved skill of the hunted* must always be close, and smallest advantages must often tip the scale). While the fore-part of the bird is beginning to move, unnoticed, his conspicuous tail, a yard behind his vital parts, catches the tiger's eye, in its earliest motion, and the tiger, seeing no other part so distinctly, springs at these long feathers, whose design is arranged for *conspicuousness in motion*.

These gorgeous birds will prove to be additionally concealed, not revealed, by their costumes. It is worth mentioning here, in connection with the Warning-Colour theory, that while Peacocks and Pheasants are *iridescent plumaged* birds, and would be called conspicuous in the highest degree, they are not *unpalatable*;—a fact that goes to strengthen my argument.

The next thing to be pointed out is that the general tendency of birds to wear longitudinal markings forward, and transverse ones aft, is an important factor of protection, especially in the case of the Pheasants and Peacocks, among whom this arrangement is very highly developed.

Any one who has tried to catch a snake in the grass will see at a glance why Nature tries to direct an enemy's attention behind the animal he is hunting. The snake for ever proves to be further on. It is hard to set one's foot far enough ahead as he moves, just as a wing-shot tends to shoot behind. Now Nature, realizing this, offers the enemy the utmost inducement to strike too far back. The strong cross-bars of the Reeves or the Copper Pheasant, while visually they cut the tail to pieces when it is still, are, as with the Peacock, by far the most visible part of the bird as soon as he moves. The reason of this is that in forward motion the longitudinal markings scarcely show, while the transverse ones become conspicuous. To prove this, any reader has only to blacken a few points an inch or so apart on a white cord, and then move the cord longitudinally, drawn tight across some aperture a few yards away, the cord being only visible where it crosses the aperture. He will see that its motion is distinguishable much farther off when the spots are in sight than when the *unmarked* cord is passing. The spots correspond to the tail-marks of the Pheasant, and the cord where it is *not* spotted represents the bird's longitudinal markings, *i. e.* his body-markings.

Before closing I beg to say that I do not mean that I am convinced that Mimicry and Common Warning Colours have no hand in these resemblances. I merely point out that the coloration of every individual of the "mimicking groups" of butterflies seems to be the best conceivable for effacing the aspect of its wearer, and also that it is perfectly conceivable that an external influence, like superabundance of certain very sweet flowers, could do the whole thing.



Thayer, Abbott Handerson. 1903. "XXVI. Protective Coloration in its relation to Mimiery, Common Warning Colours, and Sexual Selection." *Transactions of the Entomological Society of London* 51, 553–569.

<https://doi.org/10.1111/j.1365-2311.1903.tb01149.x>.

View This Item Online: <https://www.biodiversitylibrary.org/item/44059>

DOI: <https://doi.org/10.1111/j.1365-2311.1903.tb01149.x>

Permalink: <https://www.biodiversitylibrary.org/partpdf/35773>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Smithsonian

Copyright & Reuse

Copyright Status: NOT_IN_COPYRIGHT

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.