



**MIMICRY,
AND OTHER PROTECTIVE
RESEMBLANCES AMONG
ANIMALS**

ALFRED RUSSEL WALLACE

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**BY
ALFRED RUSSEL WALLACE**

Mimicry, and Other Protective Resemblances Among Animals by Alfred Russel Wallace.

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although they have important structural differences, and cannot be placed near each other in any natural arrangement. As a proof that the resemblance is really deceptive, it may be mentioned that the *Mimeta* is figured and described as a honeysucker in the costly "Voyage de l'Astrolabe," under the name of *Philedon bouruensis*!

Passing to the island of Ceram, we find allied species of both genera. The *Tropidorhynchus subcornutus* is of an earthy brown colour washed with yellow ochre, with bare orbits, dusky cheeks, and the usual pale recurved nape-ruff. The *Mimeta forsteni* is absolutely identical in the tints of every part of the body, the details of which are imitated in the same manner as in the Bouru birds already described. In two other islands there is an approximation towards mimicry, although it is not so perfect as in the two preceding cases. In Timor the *Tropidorhynchus timoriensis* is of the usual earthy brown above, with the nape-ruff very prominent, the cheeks black, the throat nearly white, and the whole under surface pale whitish brown. These various tints are all well reproduced in *Mimeta virescens*, the chief want of exact imitation being that the throat and breast of the *Tropidorhynchus* has a very scaly appearance, being covered with rigid pointed feathers which are not imitated in the *Mimeta*, although there are signs of faint dusky spots which may easily furnish the groundwork of a more exact imitation by the continued survival of favourable variations in the same direction. There is also a large knob at the base of the bill of the *Tropidorhynchus* which is not at all imitated by the *Mimeta*. In the island of Morty (north of Gilolo) there exists the *Tropidorhynchus fuscicapillus*, of a dark sooty brown colour, especially on the head, while the under parts are rather lighter, and the characteristic ruff of the nape is wanting. Now it is curious that in the adjacent island of Gilolo should be found the *Mimeta phæochromus*, the upper surface of which is of exactly the same dark sooty tint as the *Tropidorhynchus*, and is the only known species that is of such a dark colour. The under side is not quite light enough, but it is a good approximation. This *Mimeta* is a rare bird, and may very probably exist in Morty, though not yet found there; or, on the other hand, recent changes in physical geography may have led to the restriction of the *Tropidorhynchus* to that island, where it is very common.

Here, then, we have two cases of perfect mimicry and two others of good approximation, occurring between species of the same two genera of birds; and in three of these cases the pairs that resemble each other are found together in the same island, and to which they are peculiar. In all these cases the *Tropidorhynchus* is rather larger than the *Mimeta*, but the difference is not beyond the limits of variation in species, and the two genera are somewhat alike in form and proportion. There are, no doubt, some special enemies by which many small birds are attacked, but which are afraid of the *Tropidorhynchus* (probably some of the hawks), and thus it becomes advantageous for the weak *Mimeta* to resemble the strong, pugnacious, noisy, and very abundant *Tropidorhynchus*.

My friend, Mr. Osbert Salvin, has given me another interesting case of bird mimicry. In the neighbourhood of Rio Janeiro is found an insect-eating hawk (*Harpagus diodon*), and in the same district a bird-eating hawk (*Accipiter pileatus*) which closely resembles it. Both are of the same ashy tint beneath, with the thighs and under wing-coverts reddish brown, so that when on the wing and seen from below they are undistinguishable. The curious point, however, is that the *Accipiter* has a much wider range than the *Harpagus*, and in the regions where the insect-eating species is not found it no longer resembles it, the under wing-coverts varying to white; thus indicating that the red-brown colour is kept true by its being useful to the *Accipiter* to be mistaken for the insect-eating species, which birds have learnt not to be afraid of.

MIMICRY AMONG MAMMALS

Among the Mammalia the only case which may be true mimicry is that of the insectivorous genus *Cladobates*, found in the Malay countries, several species of which very closely resemble squirrels. The size is about the same, the long bushy tail is carried in the same way, and the colours are very similar. In this case the use of the resemblance must be to enable the *Cladobates* to approach the insects or small birds on which it feeds, under the disguise of the harmless fruit-eating squirrel.

OBJECTIONS TO MR. BATES' THEORY OF MIMICRY

Having now completed our survey of the most prominent and remarkable cases of mimicry that have yet been noticed, we must say something of the objections that have been made to the theory of their production given by Mr. Bates, and which we have endeavoured to illustrate and enforce in the preceding pages. Three counter explanations have been proposed.

Professor Westwood admits the fact of the mimicry and its probable use to the insect, but maintains that each species was created a mimic for the purpose of the protection thus afforded it. Mr. Andrew Murray, in his paper on the "Disguises of Nature," inclines to the opinion that similar conditions of food and of surrounding circumstances have acted in some unknown way to produce the resemblances; and when the subject was discussed before the Entomological Society of London, a third objection was added — that heredity or the reversion to ancestral types of form and colouration, might have produced many of the cases of mimicry.

Against the special creation of mimicking species there are all the objections and difficulties in the way of special creation in other cases, with the addition of a few that are peculiar to it. The most obvious is, that we have gradations of mimicry and of protective resemblance — a fact which is strongly suggestive of a natural process having been at work. Another very serious objection is, that as mimicry has been shown to be useful only to those species and groups which are rare and probably dying out, and would cease to have any effect should the proportionate abundance of the two species be reversed, it follows that on the special-creation theory the one species must have been created plentiful, the other rare; and, notwithstanding the many causes that continually tend to alter the proportions of species, these two species must have always been specially maintained at their respective proportions, or the very purpose for which they each received their peculiar characteristics would have completely failed. A third difficulty is, that although it is very easy to understand how mimicry may be brought about by variation and the survival of the fittest, it seems a very strange thing for a Creator to protect an animal by making it

imitate another, when the very assumption of a Creator implies his power to create it so as to require no such circuitous protection. These appear to be fatal objections to the application of the special-creation theory to this particular case.

The other two supposed explanations, which may be shortly expressed as the theories of “similar conditions” and of “heredity,” agree in making mimicry, where it exists, an adventitious circumstance not necessarily connected with the well-being of the mimicking species. But several of the most striking and most constant facts which have been adduced, directly contradict both those hypotheses. The law that mimicry is confined to a few groups only is one of these, for “similar conditions” must act more or less on all groups in a limited region, and “heredity” must influence all groups related to each other in an equal degree. Again, the general fact that those species which mimic others are rare, while those which are imitated are abundant, is in no way explained by either of these theories, any more than is the frequent occurrence of some palpable mode of protection in the imitated species. “Reversion to an ancestral type” no way explains why the imitator and the imitated always inhabit the very same district, whereas allied forms of every degree of nearness and remoteness generally inhabit different countries, and often different quarters of the globe; and neither it, nor “similar conditions,” will account for the likeness between species of distinct groups being superficial only — a disguise, not a true resemblance; for the imitation of bark, of leaves, of sticks, of dung; for the resemblance between species in different orders, and even different classes and subkingdoms; and finally, for the graduated series of the phenomena, beginning with a general harmony and adaptation of tint in autumn and winter moths and in arctic and desert animals, and ending with those complete cases of detailed mimicry which not only deceive predacious animals, but puzzle the most experienced insect collectors and the most learned entomologists.

MIMICRY BY FEMALE INSECTS ONLY

But there is yet another series of phenomena connected with this subject, which considerably strengthens the view here adopted, while it seems quite incompatible with either of the other hypotheses; namely, the relation of protective colouring and mimicry to the sexual differences of animals. It will be clear to every one that if two animals, which as regards “external conditions” and “hereditary descent,” are exactly alike, yet differ remarkably in colouration, one resembling a protected species and the other not, the resemblance that exists in one only can hardly be imputed to the influence of external conditions or as the effect of heredity. And if, further, it can be proved that the one requires protection more than the other, and that in several cases it is that one which mimics the protected species, while the one that least requires protection never does so, it will afford very strong corroborative evidence that there is a real connexion between the necessity for protection and the phenomenon of mimicry. Now the sexes of insects offer us a test of the nature here indicated, and appear to furnish one of the most conclusive arguments in favour of the theory that the phenomena termed “mimicry” are produced by natural selection.

The comparative importance of the sexes varies much in different classes of animals. In the higher vertebrates, where the number of young produced at a birth is small and the same individuals breed many years in succession, the preservation of both sexes is almost equally important. In all the numerous cases in which the male protects the female and her offspring, or helps to supply them with food, his importance in the economy of nature is proportionately increased, though it is never perhaps quite equal to that of the female. In insects the case is very different; they pair but once in their lives, and the prolonged existence of the male is in most cases quite unnecessary for the continuance of the race. The female, however, must continue to exist long enough to deposit her eggs in a place adapted for the development and growth of the progeny. Hence there is a wide difference in the need for protection in the two sexes; and we should, therefore, expect to find that in some cases the special protection given to the female

was in the male less in amount or altogether wanting. The facts entirely confirm this expectation. In the spectre insects (Phasmidæ) it is often the females alone that so strikingly resemble leaves, while the males show only a rude approximation. The male *Diadema misippus* is a very handsome and conspicuous butterfly, without a sign of protective or imitative colouring, while the female is entirely unlike her partner, and is one of the most wonderful cases of mimicry on record, resembling most accurately the common *Danais chrysippus*, in whose company it is often found. So in several species of South American *Pieris*, the males are white and black, of a similar type of colouring to our own “cabbage” butterflies, while the females are rich yellow and buff, spotted and marked so as exactly to resemble species of *Heliconidæ* with which they associate in the forest. In the Malay archipelago is found a *Diadema* which had always been considered a male insect on account of its glossy metallic-blue tints, while its companion of sober brown was looked upon as the female. I discovered, however, that the reverse is the case, and that the rich and glossy colours of the female are imitative and protective, since they cause her exactly to resemble the common *Euploea midamus* of the same regions, a species which has been already mentioned in this essay as mimicked by another butterfly, *Papilio paradoxa*. I have since named this interesting species *Diadema anomala* (see the Transactions of the Entomological Society, 1869, p. 285). In this case, and in that of *Diadema misippus*, there is no difference in the habits of the two sexes, which fly in similar localities; so that the influence of “external conditions” cannot be invoked here as it has been in the case of the South American *Pieris pyrrha* and allies, where the white males frequent open sunny places, while the *Heliconia*-like females haunt the shades of the forest.

We may impute to the same general cause (the greater need of protection for the female, owing to her weaker flight, greater exposure to attack, and supreme importance)—the fact of the colours of female insects being so very generally duller and less conspicuous than those of the other sex. And that it is chiefly due to this cause rather than to what Mr. Darwin terms “sexual selection” appears to be shown by the otherwise inexplicable fact, that in the groups which have a protection of any kind independent of concealment, sexual differences of colour are either quite wanting or

slightly developed. The Heliconidæ and Danaidæ, protected by a disagreeable flavour, have the females as bright and conspicuous as the males, and very rarely differing at all from them. The stinging Hymenoptera have the two sexes equally well coloured. The Carabidæ, the Coccinellidæ, Chrysomelidæ, and the Telephori have both sexes equally conspicuous, and seldom differing in colours. The brilliant Curculios, which are protected by their hardness, are brilliant in both sexes. Lastly, the glittering Cetoniadæ and Buprestidæ, which seem to be protected by their hard and polished coats, their rapid motions, and peculiar habits, present few sexual differences of colour, while sexual selection has often manifested itself by structural differences, such as horns, spines, or other processes.

CAUSE OF THE DULL COLOURS OF FEMALE BIRDS

The same law manifests itself in Birds. The female while sitting on her eggs requires protection by concealment to a much greater extent than the male; and we accordingly find that in a large majority of the cases in which the male birds are distinguished by unusual brilliancy of plumage, the females are much more obscure, and often remarkably plain-coloured. The exceptions are such as eminently to prove the rule, for in most cases we can see a very good reason for them. In particular, there are a few instances among wading and gallinaceous birds in which the female has decidedly more brilliant colours than the male; but it is a most curious and interesting fact that in most if not all these cases the males sit upon the eggs; so that this exception to the usual rule almost demonstrates that it is because the process of incubation is at once very important and very dangerous, that the protection of obscure colouring is developed. The most striking example is that of the gray phalarope (*Phalaropus fulicarius*). When in winter plumage, the sexes of this bird are alike in colouration, but in summer the female is much the most conspicuous, having a black head, dark wings, and reddish-brown back, while the male is nearly uniform brown, with dusky spots. Mr. Gould in his "Birds of Great Britain" figures the two sexes in both winter and summer plumage, and remarks on the strange peculiarity of the usual colours of the two sexes being reversed, and also on the still more curious fact that the "male alone sits on the eggs," which are deposited on the bare ground. In another British bird, the dotterell, the female is also larger and more brightly-coloured than the male; and it seems to be proved that the males assist in incubation even if they do not perform it entirely, for Mr. Gould tells us, "that they have been shot with the breast bare of feathers, caused by sitting on the eggs." The small quail-like birds forming the genus *Turnix* have also generally large and bright-coloured females, and we are told by Mr. Jerdon in his "Birds of India" that "the natives report that during the breeding season the females desert their eggs and associate in flocks while the males are employed in hatching the eggs." It is also an ascertained fact, that the females are more bold and pugnacious than the males. A

further confirmation of this view is to be found in the fact (not hitherto noticed) that in a large majority of the cases in which bright colours exist in both sexes incubation takes place in a dark hole or in a dome-shaped nest. Female kingfishers are often equally brilliant with the male, and they build in holes in banks. Bee-eaters, trogons, motmots, and toucans, all build in holes, and in none is there any difference in the sexes, although they are, without exception, showy birds. Parrots build in holes in trees, and in the majority of cases they present no marked sexual difference tending to concealment of the female. Woodpeckers are in the same category, since though the sexes often differ in colour, the female is not generally less conspicuous than the male. Wagtails and titmice build concealed nests, and the females are nearly as gay as their mates. The female of the pretty Australian bird *Pardalotus punctatus*, is very conspicuously spotted on the upper surface, and it builds in a hole in the ground. The gay-coloured hang-nests (*Icterinæ*) and the equally brilliant tanagers may be well contrasted; for the former, concealed in their covered nests, present little or no sexual difference of colour — while the open-nested tanagers have the females dull-coloured and sometimes with almost protective tints. No doubt there are many individual exceptions to the rule here indicated, because many and various causes have combined to determine both the colouration and the habits of birds. These have no doubt acted and re-acted on each other; and when conditions have changed one of these characters may often have become modified, while the other, though useless, may continue by hereditary descent an apparent exception to what otherwise seems a very general rule. The facts presented by the sexual differences of colour in birds and their mode of nesting, are on the whole in perfect harmony with that law of protective adaptation of colour and form, which appears to have checked to some extent the powerful action of sexual selection, and to have materially influenced the colouring of female birds, as it has undoubtedly done that of female insects.

USE OF THE GAUDY COLOURS OF MANY CATERPILLARS

Since this essay was first published a very curious difficulty has been cleared up by the application of the general principle of protective colouring. Great numbers of caterpillars are so brilliantly marked and coloured as to be very conspicuous even at a considerable distance, and it has been noticed that such caterpillars seldom hide themselves. Other species, however, are green or brown, closely resembling the colours of the substances on which they feed, while others again imitate sticks, and stretch themselves out motionless from a twig so as to look like one of its branches. Now, as caterpillars form so large a part of the food of birds, it was not easy to understand why any of them should have such bright colours and markings as to make them specially visible. Mr. Darwin had put the case to me as a difficulty from another point of view, for he had arrived at the conclusion that brilliant colouration in the animal kingdom is mainly due to sexual selection, and this could not have acted in the case of sexless larvæ. Applying here the analogy of other insects, I reasoned, that since some caterpillars were evidently protected by their imitative colouring, and others by their spiny or hairy bodies, the bright colours of the rest must also be in some way useful to them. I further thought that as some butterflies and moths were greedily eaten by birds while others were distasteful to them, and these latter were mostly of conspicuous colours, so probably these brilliantly coloured caterpillars were distasteful, and therefore never eaten by birds. Distastefulness alone would however be of little service to caterpillars, because their soft and juicy bodies are so delicate, that if seized and afterwards rejected by a bird they would almost certainly be killed. Some constant and easily perceived signal was therefore necessary to serve as a warning to birds never to touch these uneatable kinds, and a very gaudy and conspicuous colouring with the habit of fully exposing themselves to view becomes such a signal, being in strong contrast with the green or brown tints and retiring habits of the eatable kinds. The subject was brought by me before the Entomological Society (see Proceedings, March 4th, 1867), in order that those members having opportunities for making observations

might do so in the following summer; and I also wrote a letter to the *Field* newspaper, begging that some of its readers would cooperate in making observations on what insects were rejected by birds, at the same time fully explaining the great interest and scientific importance of the problem. It is a curious example of how few of the country readers of that paper are at all interested in questions of simple natural history, that I only obtained one answer from a gentleman in Cumberland, who gave me some interesting observations on the general dislike and abhorrence of all birds to the "Gooseberry Caterpillar," probably that of the Magpie-moth (*Abraxas grossulariata*). Neither young pheasants, partridges, nor wild-ducks could be induced to eat it, sparrows and finches never touched it, and all birds to whom he offered it rejected it with evident dread and abhorrence. It will be seen that these observations are confirmed by those of two members of the Entomological Society to whom we are indebted for more detailed information.

In March, 1869, Mr. J. Jenner Weir communicated a valuable series of observations made during many years, but more especially in the two preceding summers, in his aviary, containing the following birds of more or less insectivorous habits:— Robin, Yellow-Hammer, Reed-bunting, Bullfinch, Chaffinch, Crossbill, Thrush, Tree-Pipit, Siskin, and Redpoll. He found that hairy caterpillars were uniformly rejected; five distinct species were quite unnoticed by all his birds, and were allowed to crawl about the aviary for days with impunity. The spiny caterpillars of the Tortoiseshell and Peacock butterflies were equally rejected; but in both these cases Mr. Weir thinks it is the taste, not the hairs or spines, that are disagreeable, because some very young caterpillars of a hairy species were rejected although no hairs were developed, and the smooth pupæ of the above-named butterflies were refused as persistently as the spined larvæ. In these cases, then, both hairs and spines would seem to be mere signs of uneatableness.

His next experiments were with those smooth gaily-coloured caterpillars which never conceal themselves, but on the contrary appear to court observation. Such are those of the Magpie moth (*Abraxas grossulariata*), whose caterpillar is conspicuously white and black spotted — the *Diloba coeruleocephala*, whose larvæ is pale yellow with a broad blue or green

lateral band — the *Cucullia verbasci*, whose larvæ is greenish white with yellow bands and black spots, and *Anthrocera filipendulæ* (the six spot Burnet moth), whose caterpillar is yellow with black spots. These were given to the birds at various times, sometimes mixed with other kinds of larvæ which were greedily eaten, but they were in every case rejected apparently unnoticed, and were left to crawl about till they died.

The next set of observations were on the dull-coloured and protected larvæ, and the results of numerous experiments are thus summarised by Mr. Weir. “All caterpillars whose habits are nocturnal, which are dull coloured, with fleshy bodies and smooth skins, are eaten with the greatest avidity. Every species of green caterpillar is also much relished. All Geometræ, whose larvæ resemble twigs as they stand out from the plant on their anal prolegs, are invariably eaten.”

At the same meeting Mr. A. G. Butler, of the British Museum, communicated the results of his observations with lizards, frogs, and spiders, which strikingly corroborate those of Mr. Weir. Three green lizards (*Lacerta viridis*) which he kept for several years, were very voracious, eating all kinds of food, from a lemon cheesecake to a spider, and devouring flies, caterpillars, and humble bees; yet there were some caterpillars and moths which they would seize only to drop immediately. Among these the principal were the caterpillar of the Magpie moth (*Abraxas grossulariata*) and the perfect six spot Burnet moth (*Anthrocera filipendulæ*). These would be first seized but invariably dropped in disgust, and afterwards left unmolested. Subsequently frogs were kept and fed with caterpillars from the garden, but two of these — that of the before-mentioned Magpie moth, and that of the V. moth (*Halia wavarica*), which is green with conspicuous white or yellow stripes and black spots — were constantly rejected. When these species were first offered, the frogs sprang at them eagerly and licked them into their mouths; no sooner, however, had they done so than they seemed to be aware of the mistake that they had made, and sat with gaping mouths, rolling their tongues about until they had got quit of the nauseous morsels.

With spiders the same thing occurred. These two caterpillars were repeatedly put into the webs both of the geometrical and hunting spiders (*Epeira diadema* and *Lycosa* sp.), but in the former case they were cut out

and allowed to drop; in the latter, after disappearing in the jaws of their captor down his dark silken funnel, they invariably reappeared, either from below or else taking long strides up the funnel again. Mr. Butler has observed lizards fight with and finally devour humble bees, and a frog sitting on a bed of stone-crop leap up and catch the bees which flew over his head, and swallow them, in utter disregard of their stings. It is evident, therefore, that the possession of a disagreeable taste or odour is a more effectual protection to certain conspicuous caterpillars and moths, than would be even the possession of a sting.

The observations of these two gentlemen supply a very remarkable confirmation of the hypothetical solution of the difficulty which I had given two years before. And as it is generally acknowledged that the best test of the truth and completeness of a theory is the power which it gives us of prevision, we may I think fairly claim this as a case in which the power of prevision has been successfully exerted, and therefore as furnishing a very powerful argument in favour of the truth of the theory of Natural Selection.

SUMMARY

I have now completed a brief, and necessarily very imperfect, survey of the various ways in which the external form and colouring of animals is adapted to be useful to them, either by concealing them from their enemies or from the creatures they prey upon. It has, I hope, been shown that the subject is one of much interest, both as regard a true comprehension of the place each animal fills in the economy of nature, and the means by which it is enabled to maintain that place; and also as teaching us how important a part is played by the minutest details in the structure of animals, and how complicated and delicate is the equilibrium of the organic world.

My exposition of the subject having been necessarily somewhat lengthy and full of details, it will be as well to recapitulate its main points.

There is a general harmony in nature between the colours of an animal and those of its habitation. Arctic animals are white, desert animals are sand-coloured; dwellers among leaves and grass are green; nocturnal animals are dusky. These colours are not universal, but are very general, and are seldom reversed. Going on a little further, we find birds, reptiles, and insects, so tinted and mottled as exactly to match the rock, or bark, or leaf, or flower, they are accustomed to rest upon — and thereby effectually concealed. Another step in advance, and we have insects which are formed as well as coloured so as exactly to resemble particular leaves, or sticks, or mossy twigs, or flowers; and in these cases very peculiar habits and instincts come into play to aid in the deception and render the concealment more complete. We now enter upon a new phase of the phenomena, and come to creatures whose colours neither conceal them nor make them like vegetable or mineral substances; on the contrary, they are conspicuous enough, but they completely resemble some other creature of a quite different group, while they differ much in outward appearance from those with which all essential parts of their organization show them to be really closely allied. They appear like actors or masqueraders dressed up and painted for amusement, or like swindlers endeavouring to pass themselves off for well-

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