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ATTEMPTS TO DISPROVE THE THEORIES OF WARNING COLOURS, MIMICRY AND PROTECTIVE RESEMBLANCE IN INSECTS

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About twenty years ago, in a paper (1) written by Dr. W. L. Mc Atee, the attempt was made to disprove the value of experiments by which many naturalists had tested and, as they believed, confirmed the theories of Warning Colours, Mimicry and Protective Resemblance in insects. In an address (2) to the Zoological Section of the British Association in 1931, I admitted a probable mistake « in not at once writing a detailed reply to these criticisms, which were not only directed against the conclusions drawn from experimental feeding, but also against other conclusions on which the theory of mimicry is founded. On the other hand, there was much to be said for waiting until far more evidence had been collected, and now, after nearly twenty years, it may be fairly maintained that such evidence has been forthcoming. » (p. 90).

A more important reason for delay was a discussion (3) held in 1897, in which certain experienced naturalists and travellers stated that they had never seen a Butterfly captured or even attacked by a bird. This surprising result and the valuable paper (4) by Sir Guy Marshall in 1909, called for

(1) « The Experimental Method of Testing the Efficiency of Warning and Cryptic Coloration in Protecting Animals from their Enemies. » *Proc. Acad. Nat. Sci. Phila.*, June 1912, pp. 281-364 (issued 6 Sept. 1912).

(2) « A Hundred Years of Evolution », *Rep. Brit. Assoc. Adv. Sci.*, Centenary Meeting, 1931, pp. 71-95.

(3) *Proceedings of the Entomological Society of London*, 1897, pp. xiii-xxvi. Future references to this publication will be in this form « *Proc.* », followed by the year and page or pages, also, after 1925, by the volume.

(4) « Birds as a Factor in the Production of Mimetic Resemblances among Butterflies », *Transactions of the Entomological Society of London*, 1909, pp. 329-383. Future references to this publication to be in this form « *Trans.* », followed by the year and page or pages.

extended observations specially directed to this subject, and it was considered better to postpone further discussion until far more data had accumulated. Dr. McAtee is entirely mistaken in his opinion, expressed in a later paper (5), that « the contentions of the article on the experimental study of the food habits of animals seem to have been generally admitted, or at least regarded as too well supported to be lightly attacked » (p. 2). Some of his contentions in both papers are disproved in later pages, and others will, I believe, be disproved in a future publication.

Referring to the theories of Warning Colours and Mimicry, Dr. McAtee wrote (1 : p. 282) : « Each of these theories ..... was built up in the absence of evidence that the insects concerned were actually distasteful or palatable as claimed. This was the principal criticism made by the comparatively few who at the time dared question the all-sufficiency of natural selection, and it stands to-day the greatest obstacle to acceptance of the theories ».

Naturally hypothesis must be born before it is tested, but in these instances the test followed quickly and was promoted from the first. The history is briefly as follows : — Darwin writing to Wallace, 23 February, 1867, asked if he could explain why Caterpillars are « sometimes so beautifully and artistically coloured? » Wallace's prompt reply was an account of his hypothesis of Warning Colours which even then had been to some extent tested, for Darwin wrote on February 26th, « I never heard anything more ingenious than your suggestion, and I hope you may be able to prove it true. That is a splendid fact about the white moths; it warms one's very blood to see a theory thus almost proved to be true (6) ». Wallace did not delay in seeking proofs. In a week he brought the subject before the Entomological Society of London (7), « in order that those members having opportunities for making observations might do so in the following summer », and also wrote to the *Field* with the same object (8).

In two years the results of numerous experiments, conducted by J. Jenner Weir (9) and A. G. Butler (10), were published, these and the later experiments of Prof. August Weismann, and still later my own, being brought together in a single paper (11) which appeared in 1887. These facts are well known but I have ventured to mention them briefly on the present occasion, inasmuch as Dr. McAtee's statement quoted above, conveys an unfair impression of

(5) « Effectiveness in Nature of the So-called Protective Adaptations in the Animal Kingdom, chiefly as Illustrated by the Food Habits of Nearctic Birds ». Smithsonian Miscellaneous Collections. Vol. 85, No. 7 (Publication 3125), published 15 March, 1932, pp. 1-201.

(6) « Life and Letters of Charles Darwin », London, 1887, vol. III, pp. 93, 94, for this and the letter of February 23rd.

(7) *Proc.*, 1867, p. lxxx.

(8) « On Natural Selection », London, 1875 edn., p. 119.

(9) *Trans.*, 1869, p. 21.

(10) *Trans.*, 1869, p. 27.

(11) *Proc. Zool. Soc. Lond.*, 1887, pp. 191-274.

the scientific spirit in which Wallace's hypothesis was brought before the world.

The experimental basis of the theory of Warning Colours, and incidentally of Mimicry and Protective Resemblance — for differential food preferences are the foundation of all these theories — was further investigated with results which appeared in books and papers by the following writers, in the order of publication. — E. B. Poulton [12], F. E. Beddard ([13]), C. Lloyd Morgan ([14]), G. A. K. Marshall ([15]) (with E. B. Poulton), and R. I. Pocock ([16]). Other shorter papers on the same subject are quoted in some of these publications, and need not be mentioned separately.

The conclusions formed by all the trained naturalists who, from time to time, between 1867 and 1912, had experimented upon the insect-food-preferences of captive animals are dismissed by Dr. McAtee as « imaginative inferences from abnormal behaviour » (1 : p. 364). The author, however, was not unwilling to make such experiments himself and even to deduce from them the most highly « imaginative inference ». I refer to the food offered to his « partially domesticated » toad, which accepted all the stinging insects offered to him « although at times he showed considerable but ludicrous signs of discomfort. Not less than 30, and perhaps as many as 40 Hymenoptera were taken by this animal in about an hour. He finally left the spot, apparently to get away from a locality characterized by such extremely spicy food, which nevertheless he was apparently unable to refuse » (1 : p. 291). Perhaps, however, Dr. McAtee intended this as a joke.

In the succeeding interval, between 1912 and 1932 when Dr. McAtee's second paper appeared, far more experiments were made and supported by observations on the behaviour of animals in the wild or semi-wild condition.

The principal publications in this country and in Ceylon, in the order of their appearance, are by the following writers : C. F. M. Swynnerton ([17-18]),

(12) « Colours of Animals », Internat. Sci. Ser., Lond., 1890, pp. 159-215.
(13) « Animal Coloration », Lond,, 1892, chapters iv and v, pp. 148-192.
(14) Habit and Instinct, Lond., 1896, chapter ii, pp. 29-58.
(15) « Five Years Observations and Experiments (1896-1901) on the Bionomics of South African Insects, chiefly directed to the Investigation of Mimicry and Warning Colours ». *Trans.*. 1902, pp. 287-584.
(16) « On the Palatability of some British Insects, with Notes on the Significance of Mimetic Resemblances ». *Proc. Zool. Soc. Lond.*, 1911, pp. 809-864. With Notes by E. B. Poulton, pp. 865-868.
(17) « A Brief Preliminary Statement of a few of the Results of Five Years' Special Testing of the Theories of Mimicry. » A contribution to a discussion on mimicry reported in *Proc.*, 1915, pp. xxiii-xliv.
(18) « Experiments and Observations on the Explanation of Form and Colouring, 1908 1913. » *Linn. Soc. Journ.-Zool.*, vol. 33, 1919, pp. 203-385.

G. D. Hale Carpenter [19], E. B. Poulton [20], C. R. S. Pitman [21], J. G. Myers [22], and W. W. A. Phillips [23-24].

All these papers contain, like those which appeared before 1912, the recorded observations of keen naturalists, with a real love of animals, and, when there is a conflict of opinion upon the interpretation of behaviour, their conclusions are likely to be sounder than those of a writer who has devoted so much time and attention to the tabulation of the contents, first of 48,000, and then of 80,000 birds' stomachs. Not that I would undervalue this work — far from it; my only regret is that it has not been better carried out and given us fuller information about the chief enemies of insects. But the method employed, one attaching the same value to a stomach containing a single insect as to one containing hundreds, withholds from the reader precisely that information which he most desires to receive, and he learns more from the general statements in which some of the large numbers contained in single stomachs are mentioned — although without any means of learning the relative frequency of such well-filled stomachs in any species — than from the vast array of figures in the tables themselves. Further information of great importance is also wanting — whether the young were being fed and whether there was a scarcity or a superabundance of insect life at the time when the birds were shot. In periods of food deficiency single insects or very small numbers — occasionally even large numbers — would probably throw but little light upon the species of birds which are habitual enemies of the insects they had swallowed in such times of stress. If the opportunity were to arise, it would be most interesting to test in captivity the birds which there is most reason to believe are the special enemies of certain insects, and thus to determine on solid grounds the value of the experimental method as applied to the species concerned.

The *general* agreement between the results of observations and experiments recorded in the previously cited papers will, I think, be convincing to any unbiassed reader. The rejection of gaudily coloured insects by different classes of insectivorous animals is again and again contrasted with their acceptance of species bearing a Protective Resemblance to their surroundings. Exceptions in the latter category were rarely found, but not

(19) « Experiments on the Relative Edibility of Insects, with Special Reference to their Coloration. » *Trans.*, 1921, pp. 1-105.

(20) « British Insectivorous Bats and their Prey. » *Proc. Zool. Soc. Lond.*, pt. 2, 1929, pp. 277-303.

(21) « Experiments with Insect-food on the African Lemur *Perodicticus potto*, Lesson. » *Proc.*, vol. IV, 1929, pp. 90, 91; vol. V, 1930, pp. 84, 91, 92.

(22) « Observations on the Insect-food of the Coati. » *Proc.*, vol. V, 1930. pp. 69-75.

(23) « The Food of the Ceylon Slender Loris (*Loris tardigradus*) in Captivity. » *Spolia Zelanica*, 4 May, 1931, vol. XVI, pt. 2, pp. 205-208.

(24) « Feeding Experiments with Lepidoptera conducted by W. W. A. Phillips on a Ceylon Lemur. » *Proc.*, vol. VII, 1932, pp. 32-35, 49, 50.

uncommonly in the former, as we should expect in captive animals deprived of their accustomed quantity and variety of insect food, and also to be explained by the varying food-habits of different species. Furthermore, Dr. McAtee's contention that these experimental tests are « not trustworthy indications of what occurs under natural conditions » (5 : p. 2) is entirely refuted by many of the records and by comparison with observations on wild animals. Thus Dr. Hale Carpenter used to take his tame monkey out « on a long lead, note-book in hand, and note down exactly what he did, what he ate, and what he did not eat..... Under these almost natural conditions one got most interesting results, and saw how M. avoided insects that had the appearance of inedibility, and how remarkably quick he was in discovering the edible species » (19 : p. 5). Again, Dr. and Mrs. Myers' Coati was observed under even more completely natural conditions — « Although never really tamed in any disciplinary sense, it became exceedingly attached to my wife, and was therefore given complete liberty in the field, since it would always follow us. On such occasions it hunted assiduously on its own account, and was occasionally given insects we had caught, but which it might also have captured itself. Its preferences, so far as insect foods are concerned, were thus observed under practically natural conditions, for the Coati is essentially a diurnal species » (22 : p. 70). Then Mr. W. W. A. Phillips' wild Loris, although such a shy sensitive animal, soon became tame enough to take insects from his fingers and feed while being watched. His experience indicated that insects are an important and perhaps essential element in its food and that the reason why these lemurs have died in captivity was because of a too exclusive fruit diet (23 : pp. 205-208). I may also mention the immensely predominant Procryptic colouring of the prey of the Long-eared Bat, as estimated from collected moths' wings, representing 1330 specimens (belonging to 182 species), of which only 16 (5 species) were other than concealed by Protective Resemblance in the resting position (20 : pp. 284-288).

It may be objected that the above-described conditions applied to insectivorous mammalia only; but the domestic fowls tested by Mr. G. L. Bates ([25]) were certainly free to follow their natural preferences, as described in his letter to Mr. W. F. H. Rosenberg : « I had been in the habit of watching the poultry that sometimes came to pick up the rejected insects thrown out on the ground. These fowls were in general not very keen for the butterflies or moths, though they were very greedy for grasshoppers that were thrown out. Most of the fowls never touch Lepidoptera after the first day or two. But the cock and the one-eyed hen thought butterflies worth taking, though they did not take them all, but selected certain ones, and often pecked and then abandoned certain kinds. » Even these

(25) « Observations in the Cameroons (1910) by Mr. G. L. Bates on the behaviour of Domestic Fowls towards rejected specimens of butterflies », etc. *Proc.*, vol. V., 1930, pp. 37-41.

two birds « got tired of butterflies after awhile, but they never ceased to like the grasshoppers..... I especially noted that the fowls appeared to reject all the Acraeas ». This last observation was confirmed by the wings of five Acraeine species all labelled « not touched », « not eaten », or « rejected ».

Mr. Bates' observations, together with those made upon the mammals (which would occupy too much space if quoted here), supply an interesting comment on Dr. McAtee's statement; — « It is the old story over again of food supplies (beetles in the present consideration) being drawn upon in proportion to their abundance and availability » (5 : p. 84). As beetles are here specially mentioned it may be added that Dr. Myers' Coati exhibited unmistakable evidence of preference between different species.

Although the observations upon wild animals are not as numerous as could be wished — or rather were not until 1930 and 1931 when Dr. F. Morton Jones carried on his researches (26) on the island of Martha's Vineyard, Massachusetts, — nevertheless striking confirmation of the conclusions derived from the feeding experiments has been supplied by scattered instances in which a butterfly or moth with a conspicuous warning pattern was seen to be refused, after seizure or examination, by a predacious enemy. The following records, with two exceptions (from the *Transactions*), are published in the *Proceedings of the Entomological Society of London,* so that is only necessary to quote the year and page.

1. *Acraea* seized and rejected by Wagtail which had caught and eaten other butterflies. Dr. S. A. Neave, nr. Entebbe, 1912, p. lv.
2. Danaine (*D. chrysippus*) eagerly seized and instantly rejected by young Fiscal Shrike (*Lanius collaris*). Rev. G. Cecil Day, Modderpoort, 1921, p. lxxiv.
3. Preference of Wagtails for Lycaenid butterflies over white Pierines « quite certain ». Dr. G. D. Hale Carpenter, W. of Victoria Nyanza, 1915, pp. lxix-lxxii; Danaine neglected, p. lxxv.
4. Danainae refused; Acraeinae sometimes refused, sometimes accepted, by spiders. G. A. K. Marshall, Natal, *Trans.,* 1902, pp. 319-325. The author remarks « In one respect spiders are extremely satisfactory for the purpose of these experiments. They remain throughout wild animals with their natural sources of food still available » (p. 325).
5. Danainae refused; Acraeinae (except *A. acara,* the species with strongest smell) and other butterflies accepted by web-building spiders. Canon K. St. Aubyn Rogers, nr. Mombasa, 1916, pp. lxxiv-lxxvi.
6. Conspicuous day-flying Hypsid moth seized and rejected by young Drongo. G. A. K. Marshall, Gazaland, *Trans.,* 1902, pp. 358, 359.

(26) « Insect Coloration and the relative acceptability of Insects to Birds. » *Trans.,* 1932, pp. 345-385.

7. Cinnabar moth (*Euchelia jacobaeae*, L.) caught on wing and rejected by Robin. R. Trimen, Woking, 1912, pp. xc, xci.
8. Conspicuous « Peach-moth » seized and dropped by « Noisy Bush-Chat » (*Cossypha*). H. Millar, Durban, 1918, pp. xxvii, xxviii.
9. Conspicuous Hypsid moth on ceiling inspected and neglected by three Geckos. W. A. Lamborn, Kuala Lumpur, 1921, p. vii.

Dr. McAtee does not mention a relatively large number of the published records here quoted, or included in the books and papers to which references have been given, while his attempts to criticize the records which he does mention are warped by an unscientific bias.

A study of Professor Lloyd Morgan's admirable « Habit and Instinct », with — if only it were possible — a little humility, would have saved us from the crude psychology of the following passage (5 : p. 3).

« Undeniably selectionists have been absurd in their disquisitions on adaptations; for instance 'eye-spots' on a butterfly's wings are to direct the attack of enemies to a non-vital spot, while 'eye-spots' on a caterpillar are 'terrifying' and prevent even a touch where a touch would be fatal. » It is strange that Dr. McAtee should not have realised that, the eye being *the* characteristic feature of a Vertebrate animal, it suggests, by association, terror in formidable animals, while stimulating and directing attack upon those which are harmless; and, corresponding with these contrasted effects, the eye is rendered conspicuous in the first class and inconspicuous in the second. The danger of this feature to its possessor was fully recognised by Gilbert White when he wrote in 1768 of the young Stone Curlews — « withdrawn to some flinty field by the dam, where they skulk among the stones, which are their best security; for their feathers are so exactly of the colour of our gray spotted flints that the most exact observer, unless he catches the eye of the young bird, may be eluded » (27).

The fact that eye-spots on butterflies' wings do in fact direct attack has been proved by careful observers who have seen the attacks delivered, and indirectly by the large numbers of otherwise fresh specimens which are found to have been injured at or near an eye-spot. Furthermore, the terror of birds, monkeys, and lizards, at the sight of the large eye-like marks of Sphingid larvae has been described by naturalists whose witness will, I believe, be generally respected although ignored by Dr. McAtee. The instances described and referred to in 15 (pp. 397-399) have recently been confirmed by Captain C. R. S. Pitman whose African Lemurs, both male and female, were terrified by a Sphingid caterpillar with large « eyes » (21 : *Proc.*, vol. IV, 1929, p. 91).

To continue Dr. McAtee's antitheses which lose all the superficial appearance of incongruity in the light shed by the principle of association :

(27) « Natural History and Antiquities of Selborne », Edited by L. C. Miall and W. Warde Fowler, London, 1901, p. 36.

— « In numerous species of birds the male is colored red and black or orange and black, characteristics that selectionists say have been developed by sexual selection as an attraction to the opposite sex, yet the females of these birds are supposed to be repelled by these same colors in possible insect prey; red insects are said to be warningly, red fruits invitingly colored, and so on. »

With equal justification the author might maintain that it is « absurd » to admire Coleridge's lines :

« The bride hath paced into the hall,
« Red as a rose is she »,

and at the same time to fix a red label on a poison-bottle and to convey a warning of danger by a red signal.

The passage referred to winds up with a criticism of the supposed inconsistency of sportsmen who, quite reasonably, « hold up to admiration the marvellous protective coloration of game birds, and in the next breath complain of severe depredations on these birds by 'vermin' ». I may in reply refer to Thomas Belt's words in a passage which is too often forgotten :

« Natural selection not only tends to pick out and preserve the forms that have protective resemblances, but to increase the perceptions of the predatory species of insects and birds, so that there is a continual progression towards a perfectly mimetic form. This progressive improvement in means of defence and of attack may be illustrated in this way. Suppose a number of not very swift hares and a number of slow-running dogs were placed on an island where there was plenty of food for the hares but none for the dogs, except the hares they could catch; the slowest of the hares would be first killed, and the swifter preserved. Then the slowest-running dogs would suffer, and having less food than the fleeter ones, would have least chance of living, and the swiftest dogs would be preserved; thus the fleetness of both dogs and hares would be gradually but surely perfected by natural selection, until the greatest speed was reached that it was possible for them to attain. I have in this supposed example confined myself to the question of speed alone, but in reality other means of pursuit and of escape would come into play and be improved[28]. »

It will be appropriate to direct attention to one or two of Dr. Mc Atee's positive *ex cathedra* pronouncements before enquiring how far his attitude is justified by a foundation of knowledge and experience.

Referring to the attacks made by a host of enemies on the Saltatoria (grasshoppers, locusts and crickets), he writes (5 : p. 38) : — « Despite persecution, these insects abound and the reasons are high fecundity and the great surplus of food available to them; these are substantial realities and

(28) « Naturalist in Nicaragua », 2nd Ed., Lond., 1888, p. 383.

outweigh immeasurably those airy intangibilities classed as protective adaptations. »

Gratiano's words rise unbidden :

« As who should say, 'I am Sir Oracle,
« And when I ope my lips let no dog bark!' »

Then again, referring to Warning Colours and Mimicry in butterflies and moths, he writes :

« As remarked in my 1912 paper, these theories were chiefly built up at a time when there was almost complete ignorance of the actual feeding habits of predacious animals, and attempts to secure evidence on the subject by experiment were in most cases characterized by a singular lack of appreciation of the vital factors involved and of realities in nature. » (5 : p. 52).

Now let us enquire how far an appreciation of these « vital factors » and « realities » is to be detected in some of Dr. McAtee's criticisms.

The well-known but wonderful procryptic resemblances of the stick-like Geometrid caterpillars, « Loopers », referred to by the present writer (12 : p. 26) and Paul Griswold Howes ([29]), are quoted by Dr. McAtee (5 : p. 53), with a reference to p. 58 (unfortunately printed « 85 »), for the following supposed refutation : — « Loopers..... are said to be protected by resemblance to twigs, etc., a statement made without giving due weight to the fact that such a defense depends upon immobility whereas these caterpillars must be in motion the greater part of the time while searching for and devouring food. » Being unwilling to follow Dr. McAtee's controversial methods and to speak of « vast ignorance » or « absurd » arguments, I will only point out that the above-quoted sentence implies an imperfect acquaintance with the knowledge possessed by every schoolboy who has bred caterpillars — the knowledge that the stick-like Geometrid larvae are only at night « in motion..... while searching for and devouring food », and that they remain still and rigid by day. Moreover, they are provided with manifold adaptations enabling them to preserve this rigidity in spite of the strain. Although this behaviour must have been observed again and again in hundreds of species it appeared to be worth while to take special notes of the times at which one of these caterpillars began to move and feed. Accordingly in May 1919, one of the finest of the British Stick-like Geometrids (*Uroptery.x sambucaria*, L.) was carefully watched on three days and found to begin feeding between 9.0 and 10.0 p.m., summer time ([30]).

([29]) « Insect Behaviour », 1919, pp. 164, 165. « Complete » immunity was probably claimed inadvertently by this naturalist. « Loopers » are certainly eaten whenever they are detected by birds. The Darwinian holds, on the principles of Belt's hypothetical example quoted on p. 40, that it was by the successful attacks of enemies that the protection has been gradually evolved and kept at a high level, when attained.

([30]) *Proc.*, 1919, pp. xxxiv-xxxvi. The following times were noted on these three days : 20 May, 9.10 p.m. — Day position (third observation); 9.43 p.m. — Eating without shift of position.

The adaptations by which these stick-like caterpillars are enabled to maintain their position by day, and the changes in position at different stages of growth are of great interest but would occupy too much space on the present occasion, and I pass on to Dr. McAtee's remarks on the resemblance of certain caterpillars to birds' excreta as pointed out in detail by P. G. Howes (29 : p. 165.) « This comment », writes Dr. McAtee (5 : p. 54, n. 1) « ignores the fact that a great many birds habitually devour the excreta of their young, even returning to it when accidentally dropped, and this nestling excreta is [sic] exactly of the luscious appearence described by Howes. » Some birds certainly act in this manner and there can be little doubt about the reason. In these species the parents, hard-pressed by the necessity for feeding their rapidly growing young, are able to extract some further nourishment from the material which has been subjected to less mature digestive processes. But what evidence is there that the excreta of birds, scattered here and there over leaves and twigs, the excreta resembled by caterpillars, as Howes and others have rightly maintained, what evidence is there of these being sought and devoured by birds or other enemies of insects? The Darwinian interpretation is furthermore strongly supported by the fact that the resemblance may be produced in very different ways — in an Indian caterpillar described by Col. A. Newnham, by form and attitude; in a rare Javan spider discovered by Dr. H. O. Forbes, in part by the spider itself and in part by its web ([31]).

The following description of this remarkable example, based upon Dr. Forbes' most interesting work([32]), was written so long ago (12 : p. 75) that it is probably unknown to many.

« The resemblance to a bird's dropping on a leaf is carried out with extraordinary detail. Such excreta consist of a 'central and denser portion, of a pure white chalk-like colour, streaked here and there with black, and surrounded by a thin border of the dried up more fluid part, which, as the leaf is rarely horizontal, often runs for a little way towards the margin' and there evaporates, forming a rather thicker extremity. The margin [border] is represented by a film-like web, with a thickened part to represent the fluid which has run to the edge or apex of the leaf; the central mass is represented by the spider itself with white abdomen and black legs, lying on

21 May, 9.20 p.m. — Day position (third observation); 9.55. — Eating vigorously in new position; body curved.

23 May, 9.30 p.m. — Day position (third observation); 9.45 p.m. — Moving about freely.

On 18 May at 6.40 p m. it was found to be gently feeding on the leaf with which its head was in contact in the day position. Not again observed till 10.45 when it had moved to a different part of the food plant.

On the following morning it was found on another twig, exhibiting no tendency to « home ». Day position maintained at 9.0 p.m.; next observation at 10.45 p.m. when it was moving about.

(31) *Proc.*, 1924, pp. xc-xciv, with references to original records.

(32) « A Naturalist's Wanderings in the Eastern Archipelago », Lond., 1885, pp. 63-65.

its back in the middle of the web, and held in position by the spines on its anterior legs which are thrust under the film. The whole combination of habits, form, and colouring afford a wonderful example of what natural selection can accomplish. »

It must be added that, butterflies being often attracted to birds' excreta, this spider (*Ornithoscatoides decipiens*) probably gains the double advantage of an Alluring and a Procryptic Colouring.

On the extremely interesting behaviour of crabs in « associating sea-anemones and ascidians with themselves », Dr. McAtee remarks : — « Both of these classes of animals have their enemies which probably would engulf crab and all in cases where the animals were together (5 : p. 22).

The improbability of this conclusion is proved by old observations and experiments which Dr. McAtee ignores. Thus Professor Walter Garstang, referring to his Plymouth experience with two species of hermit crab bearing sea-anemones on their borrowed shells, recorded in 1890, that when these Crustacea are « young and small they are obliged to live in shells without anemones », and that he « has often found them, shells and all, in the stomachs of gurnards and other fish. He has never found the larger crabs with shells suited for Actinians in the stomachs of fish » (12 : p. 203). In the same year I tested (33) one of these sea-anemones (*Sagartia*) borne by the common *Pagurus bernhardus* « by touching it with the tip of my tongue, and at once experienced a sharp smart which endured for many hours. » Pieces of the *Sagartia* thrown into one of the tanks were at first taken by a few fishes in mistake for the accustomed bits of meat, « but no sooner had one been received into the mouth, than it was shot out again with much force, and the fish shook its head violently from side to side, apparently feeling the same smart which I had experienced myself. After these first trials not one of the fish would touch the pieces. » A smaller crab, *P. cuanensis*, enclosed in an orange-red sponge (*Suberites*) was, when extracted, greedily devoured, although pieces of the sponge were even more quickly recognised and rejected than those of the sea-anemone.

It is a satisfaction to be able to bring this paper to an end by producing evidence that I am in entire agreement with one of Dr. McAtee's opinions, viz. that « the most potent protective adaptations possible do not necessarily protect » (5 : p. 75). I venture, therefore, to quote words spoken at a meeting of the Entomological Society of London on 7 May, 1913, when Mr. J. C. F. Fryer (34) brought forward extremely interesting and conclusive evidence that butterflies belonging to the most distasteful groups were

(33) *Proc. Zool. Soc. Lond.*, 1922, p. 897.

(34) « Wings of Danaine and Euploeine butterflies killed by birds in Ceylon. » *Proc.*, 1913, pp. xl., xli.

devoured by certain birds in Ceylon. I trust that the length of the passage may be excused in view of the fact that the erroneous conception of absolute immunity has taken so strong a hold upon the imagination of many naturalists.

« Professor Poulton had always combated the opinion of the late Erich Haase that protected species with warning colours enjoy 'absolute' immunity from attacks. He was confident that no species in the world enjoyed absolute immunity, and those forms with special protection and warning colours we should expect to find and did find attacked by certain special enemies able to disregard the means of defence and so gain for themselves a supply of food which was abundant, easily seen, and easily caught. We should expect to witness such attacks more readily than others, because the prey were themselves slow flying and locally abundant. Such facts were well known among the insects defended by stings, no less than in those protected by an unpleasant taste or smell. Thus bees were well known to be attacked by special birds, and a similar relationship to enemies would no doubt be found in all insects, however well defended. The same argument held with regard to procryptic colouring. It was erroneous to suppose that concealment was always efficacious; on the contrary large numbers of insect-eating vertebrates preyed habitually on insects with procryptic colouring. »

The considerations advanced in this passage go far, I believe, to reconcile conflicting views such as those held on the subject of ants — successfully attacked as they are by enemies of many and varied kinds, yet holding their own in all the habitable parts of the earth, and providing models for well-nigh innumerable mimics belonging to diverse groups of insects, as well as many in the Arachnida.

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