1929 *Proceedings* (**4** : 70). In this instance the male *urticae* was eagerly pursuing a male *A.* (*B.*) *euphrosyne* L. Mr. Andrewes' description suggests that the male was acting as he does when obeying his normal instincts and settles behind the female with his head so near to her hind-wings that he can drum upon them with the antennal knobs. (See 1930, *Proc. ent. Soc. Lond.*, **5** : 99–101, with references.)

Two rare insects from Wicken Fen. By H. St. J. K. DONISTHORPE.

In September I took a specimen of *Psectra diptera* Burm. (Neuropt. HEMEROBIIDAE) in cut sedge. Although widely distributed in the Old World, from Siberia, through Scandinavia, to the British Isles and south to Italy, it is extremely rare and only 4 specimens have been previously recorded from Britain. A remarkable feature of the genus is the extraordinary dimorphism in the development of the wings—there being two forms, one with fully developed wings and one with the hind-wings very rudimentary. I am indebted to Mr. D. E. Kimmins for the identification of this insect.

I have also taken 3 specimens of the Capsid *Cyrtorrhinus geminus* Flor. in September at the same locality. Only a few specimens have been taken previously in this country until last year (1933), when it was taken in some numbers in Staffordshire. I am indebted to Mr. W. E. China for the identification of this species.

Wednesday, 5th December, 1934.

Dr. S. A. NEAVE, O.B.E., President, in the Chair.

The SECRETARY read for the second time the nominations of the Council for Officers and Council for 1935.

Election of Fellows.

The following were elected Fellows of the Society :—WALTER WILLIAM BAUM, Hazelhurst, 68, Hillmorton Road, Rugby; ANDREW G. HAMILTON, Imperial Institute of Entomology, British Museum (Natural History), Cromwell Road, S.W.7.

Obituary.

The death of Mr. G. C. LEMAN, elected a Fellow of the Society in 1920, and of Major H. C. JEDDERE-FISHER, elected a Fellow in 1928, was announced.

Exhibits.

The following communications were made to the meeting :—

A new host record for *Phryxe vulgaris* Fall. By A. W. MCKENNY HUGHES.

I have not traced a record of *Phryxe vulgaris* Fall., as a parasite of *Borkhausenia pseudospretella* Stn. and wish therefore to record it as having been bred from a larva of this common moth.

The first recorded capture of *Argynnis maia* (Cramer) in England. By E. B. FORD.

Mr. A. W. Bennett captured a specimen of *Argynnis maia* (*pandora*) between 3–9 August, 1911, near Tintagel, Cornwall, in a valley called St. Knighton's

Kieve. It was flying with several others over a large patch of purple loose-strife, and Mr. Bennett, realising that it differed from *A. paphia*, managed to secure it with his cap. He then pinched it, and set it with an ordinary pin on a flat piece of wood. On comparing the specimen with examples of the latter species in the British collection which he had formed many years previously, it was at once evident that it differed considerably from them.

Thinking that it was of some interest, Mr. Bennett sent the specimen to a well-known Entomologist who had published a work on British butterflies and moths several years previously. He supplied him with the details of its capture, and asked him if he would kindly give him some information about it. The gentleman in question did not see fit to reply to Mr. Bennett, but sent back the specimen, writing on the brown-paper wrapper the words, "*Argynnis paphia*." On its return, one of its antennae was found to be missing.

A few years later I identified the insect from a book on European butterflies, but after his previous experience, Mr. Bennett did not feel inclined to go further with the matter. The specimen has remained in his cabinet since his death some years ago. It was shown to the meeting with a photograph, taken at the time, showing the spot where it was captured.

Habits of *Gonteosphodrus bicolor* Chees., a Reduviid from Papua. By L. Evelyn Cheesman.

The chief food of these bugs in the adult stage is bees and wasps, and they are usually found on plants or blossoms. Any vibration causes them to throw up the fore legs above the head, in which position they wait for victims: small insects are merely stabbed with the proboscis, but the fore-legs are used to strike down and hold on the ground larger bees and wasps. The thorax and legs have long, stiff hair, which is covered with a viscid fluid. From dissections of the legs made by Dr. Eltringham it is proved that there is a secreting hypoderm underneath the cuticle.

Tabanidae near Durazzo, Albania. By D. J. Lewis.

I wish to record the almost complete disappearance of Tabanid flies from the neighbourhood of the Durazzo Lagoon in Albania as a result of malaria control by measures against mosquitoes. The lagoon is a sheet of brackish water about four miles long, with extensive reed beds, and in July 1932 horse flies were abundant on the shore, biting men and cattle. Egg batches were numerous on the reeds. Only three species, *Tabanus solstitialis* Schin., *T. acuminatus* L., and *Chrysops italicus* Mg., were found although fourteen species were collected altogether in Albania. The lagoon was a breeding place of vast numbers of the malaria-carrying mosquito, *Anopheles elutus*, which have been controlled by the use of automatic tide gates which introduced sea water into the lagoon and raised its salinity. During a visit in July 1934 lasting four hours I noticed only one Tabanid in spite of the presence of cattle.

The Swarming Habits of some West African Diptera. By D. J. Lewis.

Note: The Milichiid fly whose swarming habits at Gadau, Nigeria, I described in 1934, *Proc. R. ent. Soc. Lond.*, **9** : 4, has been named *Pareccoptoma nigeriae*

Duda. The climatic conditions at Gadau at the time are described by Prof. P. A. Buxton and D. J. Lewis in 1934, *Phil. Trans. Roy. Soc.*, **224** : 175–240.

Assemblages of Coccinellid beetles ; also of the Danaid butterfly *Danaus plexippus* Linn., during hibernation or migration. By Prof. E. B. POULTON.

Miss F. J. Kirk's description * of *Coccinella bipunctata* L. assembling in her house, 52 Oakhill Road, Putney, referred to by Mr. H. Donisthorpe in our *Proceedings*, (**9** : 82), is a very interesting addition to the records of the behaviour of these beetles. Miss Kirk's ladybirds hibernated in a crevice in the ornamental plaster of the ceiling but in warmer weather left their retreat and flew about the room for hours at a time, striking the ceiling and always settling down in their old quarters. Miss Kirk has kindly informed me that all, or occasionally some, of the Coccinellids left the crevice in the evening, never in the daytime, and were back again in the morning. The fact that the deserted crevice should have been promptly regained suggests some definite stimulus—probably smell, because a small, roundish, discoloured patch marked the exact spot on which they clustered. This same resting-place was used in the following year but by very few of the beetles.

J. H. Fabre's account † of the seven-spotted ladybird assembling on Mont Ventoux suggests hibernation, but the gathering which he observed in June on the tableland of St. Armand can hardly have been for this purpose. He describes the effect of the sun's rays upon the legions of ladybirds gathered on the pedestal of a stone cross and the rocks forming its base. " They were mostly quite still, but wherever the sunbeams struck there was a continuous exchange of place between the newcomers, who wanted to find room, and those resting, who took wing only to return after a short flight." This summer assemblage which puzzled Fabre may probably be explained as an adaptation to promote cross-breeding, as suggested in our 1904 *Proceedings* (**1904** : xxii–xxvi) where many examples of Coccinellid and other gatherings are discussed.

My friend Dr. C. B. Williams has sent me the following interesting observations on the assembling of *D. plexippus*, the Monarch butterfly, described by Mr. L. McCormick-Goodhart, of Langley Park, Silver Spring, Maryland, in a letter to Capt. T. Dannreuther, R.N. :—

" 1934, *Oct.* 19.—These butterflies were in enormous quantities on Nantucket Island where my family and I spent the summer and where the prevailing summer wind is a fairly strong westerly one. In the evenings we were fascinated by the way in which they roosted on the trees by the house. The butterflies would come in from every point of the compass and promptly join their comrades on a particular section of the foliage on the side of the tree away from the wind. The flight towards the trees took about half an hour in all." A little later in the letter the writer states that " about a hundred of these active Monarchs roost every night like starlings on the three forty-foot silver Maples by the house."

* 1924, *Ent. Record*, **36** : 9–10.
† " Insect Life," Engl. transl., Macmillan, Lond., 1901, pp. 202–204.

In these fascinating assemblages various possible interpretations are to be borne in mind :—

1. *Migration*, ensuring that the bands are not scattered and dissipated; also that both sexes are represented.

2. *Hibernation*, ensuring these same conditions during and at the end of the winter sleep.

3. *Promotion of cross-breeding*, due to the assemblage at one spot of insects scattered over a wide area.

4. *Enhancement of aposematic effect*, a result suggested, as regards protective odours, by Fritz Müller, in *Kosmos*, Dec. 1877, translated by Prof. R. Meldola in our 1878 *Proceedings*, **1878 :** vi, vii.

It is obvious that two or more of these advantages of the gregarious habit are generally combined. Indeed the last-named would appear to be nearly always present.

Warning Colours and Mimicry : a Reply to Dr. McAtee.

By Hugh B. Cott, M.A., F.R.P.S., F.Z.S.

(*From the Department of Zoology, Glasgow University.*)

With Plates I–IV.

[Communicated, in the absence of the author, by Prof. Poulton, who referred to the unfairness of Dr. McAtee's criticisms, and, after reading Belt's account of the Nicaraguan frog from the rare original edition (1874), presented to the Society by the late Mrs. Meldola, recalled Darwin's opinion of the work—" It appears to me the best of all natural history journals which have ever been published."]

In the *Quarterly Review of Biology* for June, 1933 (9), there appears from the pen of Dr. McAtee a somewhat aggressive notice of my paper " On the Ecology of Tree-Frogs in the Lower Zambesi Valley, with special reference to Predatory Habits considered in relation to the Theory of Warning Colours and Mimicry " (4). Besides much that is either frivolous or irrelevant, the review is compounded so largely of misstatement and misrepresentation, that I feel bound to reply to this attack by drawing attention to some of the fallacies and extravagant assertions which it contains.

The greater part of the review consists of a criticism of one of the introductory sections in my paper, in which I discussed the appearance, habits and habitat of some East African tree-frogs and made certain tentative suggestions relating to the adaptive significance of colour in the Anura. I hope Dr. McAtee will forgive me for saying that if he had observed these tree-frogs, as I have done, in their natural surroundings in the palm forests of the Lower Zambesi, the greater part of what he says under this head would not have needed to be written.

Dr. McAtee writes at considerable length upon *Megalixalus fornasinii*, a small tree-frog wearing a bold disruptive pattern which I suggested—on the evidence of the frog's appearance in the field and of its food-habits as shown by stomach-contents —operates as an aggressive colour-scheme, enabling it to ambush active prey (Acridiidae, Odonata, Muscidae and Lepidoptera), which groups were eaten in conspicuously greater numbers by *M. fornasinii* than by any other species examined

(p. 476, Table II). We will now consider, as briefly as possible, what Dr. McAtee's criticism in this connection is worth.

On the general question of the appearance of *M. fornasinii*, his argument is irrelevant. " What matter," he asks, " to its victims whether it is frog-like or unfrog-like? It is one of the things that gets them and if they react defensively at all, it would be in relation to what the frog is—an enemy—without regard to kind." Dr. McAtee is apparently either unable or unwilling to appreciate the function of a disruptive colour scheme, which may—as every field naturalist knows—be most effective in rendering more difficult the recognition of an animal by enemies or by prey. It is easy for Dr. McAtee to deny the effectiveness of this type of camouflage; but the experience of the Great War proved that it was neither easy nor expedient to dispense with precisely this principle, which was applied in the so-called " dazzle " painting of ships with conspicuous success as a means of defence against submarine attack.

Passing from general to particular aspects of the question Dr. McAtee proceeds to criticise my observations on the stomach-contents of this frog. Referring to the ACRIDIIDAE he tells us: " The statement that they are eaten in conspicuously greater numbers by this frog than by any of the other species examined is untrue, as 7 ACRIDIIDAE were found in 360 stomachs of *Megalixalus*, or 1 to each 51·4 stomachs, while 3 were found in 122 stomachs of another frog (*Hyperolius argus*), or 1 to each 40·6 stomachs." It is often useful to read a document before stating what is contained in it. If Dr. McAtee will turn to the page concerned (p. 486) he will see that he has misstated the facts, and that 4 ACRIDIIDAE were found in 254 stomachs of *H. argus*, or 1 to each 63·5 stomachs; and, incidentally, that the only other species (*H. bayoni*) to contain *any* of these insects had a single example in 110 stomachs—a point which he conveniently omits to mention.

Dr. McAtee continues: "The Lepidoptera found in the stomachs of this frog were more than half larvae or caterpillars, mere ' worms ' to which the terms ' active, alert, rapid in flight ' most assuredly do not apply." This remark misrepresents the facts. The figures to which Dr. McAtee refers and to which I referred (Table II)—namely 26 Lepidoptera from 360 *M. fornasinii* as compared with 11 from 438 other tree-frogs—do not, of course, include larvae. They relate to adult insects only. But had Dr. McAtee been in any doubt upon this point, he could have verified the matter by turning to Table IV where the food-animals are classified, and where separate figures are given for caterpillars and adult insects.

We then read the following criticism: " Cott, while dilating on the powers of *Megalixalus* in capturing prey ' active, alert, rapid in flight,' says nothing about the much greater prevalence in the food of this frog of the feeble and partly wingless plant lice." Now this statement is, so far as I can see, quite irrelevant. It also happens to be quite untrue. I never said, or implied by what I said, that *Megalixalus* eats no food other than that which was active, etc. But I did point out (p. 503) in reference to plant lice eaten by this species that " they appear to be rarely used as food, for only eight out of 245 frogs [with recognisable stomach-contents] had eaten them, the stomachs of two frogs containing more than half the total number."

With reference to the next curious remark, which follows immediately after the above, that I have nothing to say as to why this frog fed to a considerably smaller

extent upon ants than did any of the other species—is it possible that Dr. McAtee has failed to realise that if the frog's food is made up of a larger percentage of large insects, *e.g.* ACRIDIIDAE, MUSCIDAE, etc., than that of the other frogs examined, it must eat a lower percentage of smaller insects, *e.g.* ants, which make up the main food (93–98 per cent.) of the other frogs?

Dr. McAtee next turns his attention to the question of warning colours, and we have further examples of the misleading statements, error, and prejudice with which he expresses his unfathomable antagonism to everything not in accord with his own views. In reference to *Hyperolius argus*, the females of which have a striking and distinctive colour pattern—being purplish or chocolate-brown, with large conspicuous orange black-bordered ocelli on the back and a canthal stripe of the same colour—I made the tentative suggestion that this colour-scheme may have an aposematic function. What I said was: "Were there any evidence (and at present I know of none) to show that the females are 'protected' by a poisonous secretion, then this would be cited as a good example of warning coloration. The conspicuous colour-scheme and the habit of exhibiting this to the best advantage in exposed situations certainly suggests something of the kind" (p. 478). My reviewer takes exception to this suggestion, and in doing so he attempts to improve on it with a somewhat comical suggestion of his own. He has evidently never seen the frogs upon whose appearance he speculates, for he speaks of the "eye-spots" as "almost matching some of the holes on a leaf on which it sits." If holes in leaves are circular, coloured bright orange and edged with a black margin, then I would agree with him, but holes of this description are outside my own experience.

The adaptive significance of colour, about which a good deal is known in relation to insects, has been little studied in relation to the Anura. The question is one which for reasons of space could not be considered in the paper under review, beyond reference in a general way (p. 478) to certain classes of coloration, namely procryptic coloration, special protective resemblance, flash colours, and warning colours associated with poisonous secretions, and to the habits of birds and snakes, the chief enemies of the group. In conclusion I said: "Faced as we are at present with scanty data, it is impossible to reach definite conclusions. The facts at our disposal do, however, appear to indicate clearly that we have in these batrachians phenomena which closely parallel many of those relating to procryptic and aposematic colouring in insects. It would be a study of the greatest interest to determine, by observation in the field and by experiment, to what extent the various features of adaptive coloration in the latter group find their analogy here." In order to show the close resemblance between the adaptive coloration of batrachians and insects, photographs of the former, taken during life and in entirely natural surroundings, are reproduced on plates I–IV. Procryptic resemblances to grasses and tangled vegetation (I), to leaves (II), to bark (III, fig. 1; IV, fig. 1), recall the protective colours and patterns of insects living in similar environments, while the aposematic display (III, fig. 2; IV, fig. 2) is brought about by the same bright colours and sharp contrasts with which we are familiar in insects. It will also be observed that the photographs were taken in different parts of the world.

I wish to emphasise that it is essentially only when different animals—whether frogs or insects or others—are studied in their natural surroundings that it is

possible to appreciate the significance of form, colour and pattern, and then only in the *living* creature, when these can be considered in relation to particular postures and habits, and to the habits of potential prey and enemies. As regards frogs, observations in this field are greatly needed. It must be remembered that birds and snakes, the chief enemies of frogs, hunt largely by sight. The following vivid account by Ditmars (5), which I quote in full, illustrates the important place occupied by vision in the hunting of prey by *Eutenia saurita* :—" The writer witnessed an example feeding in a belt of swampy timber. The high rasping croak of a small frog, directed his attention to the ribbon snake, about two and one-half feet long, which had grasped the frog by a hind leg. So vigorous were the frog's efforts, that it tore itself from the snake's grasp and started away in a series of rapid hops, with the reptile in pursuit. The serpent's movements were amazingly quick, and its power of vision in following the movements of the frog apparently acute. It darted after the amphibian for a distance of possibly eight feet, when the frog stopped, having secreted itself among some leaves. The snake also paused, but was all attention, with neck upraised and constantly darting tongue. It prowled about in frenzied fashion, when a movement of the frog attracted its attention, and it was instantly upon it, this time retaining its hold until the prey was swallowed." This incident is of particular interest because it illustrates the vital importance of *stillness*, without which the best obliterative coloration can be of no avail.

Dr. McAtee, as we should expect, disagrees with the analogy between adaptive coloration in frogs and insects respectively, to which I have drawn attention. He describes my attitude as " a very good one-page record of assumption, misstatement, and error even for a selectionist." The passages to which he refers in these terms are discussed below. But what interests me here is not so much his opinion of my work as his method of attacking it—which is to ignore the evidence, and then to deny that it exists. Thus, referring to the adaptive significance of colour in frogs, his first criticism is that " self-persuasion in the lack of evidence is something entirely out of place in science." Now there is no lack of evidence—even on the page to which he refers; Dr. McAtee might do well to consider whether there is a place in science for self-persuasion in spite of evidence.

His second criticism here is against my remark, " Poisonous skin-secretions are of common occurrence among the Anura. In many species they are known to furnish an effective means of defence against predatory enemies." " If the word *many* is taken at its ordinary valuation, this," he says, " is a definitely untrue statement " (p. 211). As this point is closely related to the next, I shall deal with both together below. Finally, referring to my remark that " Snakes and birds, the principal enemies of frogs, depend largely upon vision in hunting prey. There is evidence that these enemies learn to discriminate between poisonous forms and those which are good to eat," he reverts to his earlier contention that " there is no evidence of any frog being dangerously poisonous either to snake or bird predators upon it, hence the discrimination alleged is a myth." In view of the above dogmatic denials and assertions, it will be appropriate to direct attention to observations which bear directly upon these two questions.

One of the earliest observations on the efficiency of poisonous secretions in the Anura is that by Belt, the naturalist and explorer, who gives the following account of certain Nicaraguan frogs (2) :—"In the woods around Santo Domingo there are

many frogs. Some are green or brown, and imitate green or dead leaves, and live amongst foliage. Others are dirty earth-coloured, and hide in holes and under logs. All these come out only at night to feed, and they are all preyed upon by snakes and birds. In contrast with these obscurely coloured species, another little frog hops about in the day-time dressed in a bright livery of red and blue. He cannot be mistaken for any other, and his flaming vest and blue stockings show that he does not court concealment. He is very abundant in the damp woods, and I was convinced he was uneatable so soon as I made his acquaintance and saw the happy sense of security with which he hopped about. I took a few specimens home with me, and tried my fowls and ducks with them; but none would touch them. At last, by throwing down pieces of meat, for which there was a great competition amongst them, I managed to entice a young duck into snatching up one of the little frogs. Instead of swallowing it, however, it instantly threw it out of its mouth, and went about jerking its head as if trying to throw off some unpleasant taste."

Of *Bombinator igneus* Gadow says (7) : " When these toads are surprised on land, or roughly touched, they assume a most peculiar attitude. . . . In reality this is an exhibition of warning colours, to show the enemy what a dangerous animal he would have to deal with. The secretion of the skin is very poisonous, and the fire-toads are thereby well protected. I know of no creature which will eat or even harm them. I have kept numbers in a large vivarium, together with various snakes, water-tortoises, and crocodiles, but for years the little fire-bellies remained unmolested, although they shared a pond in which no other frog or newt could live without being eaten. Hungry water-tortoises stalk them under water, touch the intended prey with the nose in order to get the right scent, and then withdraw from the *Bombinator*. . . . "

The same authority tells us that the " strongly poisonous secretion " of *Dendrobates tinctorius* is said to be employed by the Indians of Columbia for poisoning their arrows, the poison acting on the central nervous system and being used especially for shooting monkeys (7).

Ditmars, whose wide experience as a field naturalist and as Curator of Reptiles in the New York Zoological Park enables him to speak with authority, says of the feeding-habits of the Black Snake (*Zamensis*) : " Frogs are also eaten, but among these are several species that the snake will grasp and immediately reject. An example of this type of batrachian is *Rana palustris*, which exudes an irritating secretion from the skin. Toads are never eaten. . . . " (5).

The poison of *Rana palustris*, the common Pickerel Frog, is also referred to by Wright, who states that it will frequently kill other species of frogs carried home in the same jar with it (12).

The effectiveness of the poison of toads is mentioned by Gadow, who says : " The milky secretion of toads protects them against many enemies, although not always against the grass-snake. A dog which has once been induced to bite a toad, suffers so severely that it will not easily repeat the experiment " (7).

Referring to the East African toad *Nectophrynoides vivipara*, Loveridge (8) states that " When killed in chloroform the large glands on the back and limbs exude a considerable quantity of poison which is as fluid as cow's milk."

Bufo marinus, the giant toad of the Amazon, is rendered formidable and well-nigh immune from predatory attack by the virulent poison of the highly developed

parotid glands. The fatal effect of the poison on would-be predators was brought to my notice all too plainly in the case of a fox terrier belonging to the Rev. A. Miles Moss, of Pará, when it inadvertently bit one of these toads and died within a few hours as a result of the poison discharged into its mouth. Of this species Noble writes that it "produces one of the most virulent poisons known among the Amphibia, one that frequently kills dogs which have not learned to leave the toad alone" (10).

Hyla venulosa, the Brazilian "flying" frog, produces, on being handled or irritated, a copious flow of whitish secretion—sticky and acrid, which cannot fail to act as a deterrent to many potential predators.

Of a related species Barbour writes as follows: "*Hyla vasta*, of Santo Domingo, has a skin poison so strong that it burns one's hands painfully when the frog is handled" (1).

Noble says of the African *Phrynomantis bifasciata*, that it also has "been found under certain circumstances temporarily to inflame the hands of the collector" (10), and that both this and the previous species produce great quantities of milky secretion.

In a recent publication Loveridge (8) also refers to the skin secretions of the gaudy and sluggish *P. bifasciata* as follows:—"I have previously drawn attention to the poisonous nature of the secretions of this frog, a further example came to my notice at Mwaya. One of my boys brought me a bag containing a mixed catch of frogs from bananas—*Hyperolius*, *Megalixalus*, *Leptopelis* and half-a-dozen *Phrynomerus* [*Phrynomantis*]. I chloroformed the whole lot in the bag. An hour later I tipped the catch out on to a table and began picking out the various species. The *Phrynomerus* had exuded a considerable amount of intensely sticky dermal secretion which had gummed the smaller *Megalixalus* together. After separating these and dropping them into water I could not get the gummy mucus off my fingers by washing and so rubbed them in the dust—as a monkey would do—then by rubbing them together shed the mucus like so much gutta-percha. Shortly afterwards irritation set in on my finger-tips, entirely comparable to the irritation produced by stinging nettles and it actually appeared to spread *within* my arm up to the elbow of the right arm. . . ."

It may be noted here that where very conspicuous colours occur in the group, they are characteristically associated with an effective means of defence, though the converse is by no means true, for other forms, such as *Hyla*, *Bufo*, *Ceratophrys*, may combine poison with cryptic coloration and habits. On the question of warning colours Gadow writes (7): "Most, if not all, Amphibia are more or less poisonous, and it is significant that many of the most poisonous, e.g. *Salamandra maculosa*, *Bombinator*, *Dendrobates*, exhibit that very conspicuous combination of yellow or orange upon a dark ground, which is so widespread a sign of poison." Further striking examples of this relationship between aposematic colour and effective poison in frogs are furnished by the red and blue frog described by Belt, by the observations (quoted below) of Budgett and Professor Graham Kerr in the case of *Phryniscus* and *Phyllomedusa*, and by the pink or vermilion, and black *Phrynomantis bifasciata*.

The foregoing observations prove the effectiveness of skin-secretions in defending certain Anura against predatory attack. I shall now recall some further observa-

tions, which besides providing additional evidence upon this point, are especially significant in relation to discrimination by predators.

The following valuable observations by Ditmars (5) throw light upon this question, and I quote in full his account of an experiment in New York Zoological Park to test the powers of discrimination in the King Cobra (*Naia bungarus*). " To test the assertion that *N. bungarus* feeds but seldom upon the Viperine snakes, possibly possessing an instinctive dread of the deep wounds liable to be inflicted by the fangs of such reptiles, the following experiment was conducted.

" A large, thick-bodied, harmless water snake (*Tropidonotus taxispilotus*), and a poisonous water moccasin (*Ancistrodon piscivorus*), of much the same proportions, were selected for the experiment during a period when the big cobra was voraciously awaiting its weekly meal of a living snake. The door of the cage was rolled back, and the poisonous snake thrown inside. The cobra made the customary rush for the food, but upon reaching the snake paused abruptly.

" This was the first time in the feeding of this king cobra in our Reptile House that he failed immediately to seize his victim and begin to swallow it. The moccasin was permitted to remain in the cage for about five minutes, during which time the cobra reared slightly from the door, and regarded it intently. To ascertain whether the cobra was hungry, a common striped snake was placed in the cage. It was grasped and swallowed without hesitation.

" The moccasin was again introduced. There was the same rush, and the same careful examination of the newcomer. This time, annoyed by the unceremonious treatment it had received, the pit-viper showed fight. Upon this display of hostility the cobra backed off hurriedly, nervously dilating its hood, and rearing upward. The moccasin was finally removed unharmed, and the large, harmless water snake was quietly placed in the cage. To the human observer it matched the moccasin closely, and made a show of temper considerably more emphatic than the former, but the cobra attacked it without an instant's hesitation and soon swallowed it. This experiment was repeated, and always with the same result. The cobra appeared to instantly distinguish the dangerous character of the poisonous snake."

Discrimination, in spite of Dr. McAtee's assertion, is no myth. That preference in the choice of food is usual with the majority of snakes is evident from Ditmars' account of the feeding-habits of *Spilotes* (5): " The species of *Spilotes* are particularly interesting in their feeding habits, as they are quite omni-carnivorous—feeding upon lizards and snakes, all types of batrachians, including the toads, *which lack of preference in the selection of prey among creatures that greatly vary in a possession of highly irritating skin secretions, is quite unusual for serpents that also prey as often as occasion permits, upon mammals and birds* " [italics mine].

The boomslang (*Dispholidus typus*) hunts for frogs in addition to its more favourite food of chamaeleons, birds, and their eggs; but it will not eat toads (6).

Budgett (3) mentions the food preferences of a grass snake, which was able to discriminate between palatable and unpalatable batrachians. A frog, *Paludicola signifera*, was put into a cage " in which were many brightly coloured frogs, including *Phryniscus nigricans* and *Phyllomedusa hypochondrialis*. In this cage was also a small grass snake. Hitherto it had taken no interest at all in the gaudy frogs in its cage; but as soon as the little *Paludicola* made its first spring, it was caught in mid air by the snake." It may be added here that the colour of *Phryniscus*

nigricans and *Phyllomedusa hypochondrialis* is in each case typically aposematic, that of the former species being black with yellow spots above, and black and scarlet beneath, while in the latter the back is green or blue, and the flanks scarlet with transverse bars of black.

Some of the earlier quoted observations relating to poisonous secretions as a means of defence may also be recalled here as further evidence of discrimination by snakes and other reptiles, *e.g.* Gadow on the immunity of the fire-bellied toad, and Ditmars on the food-habits of *Zamensis*, and by birds, *e.g.* Belt's aposematic frogs refused by fowls and ducks.

In conclusion, I may mention another clear case of discrimination for the particulars of which I am indebted to Professor Graham Kerr. This relates to a Seriema (*Cariama cristata*) which was kept as a pet in the Paraguayan Chaco. The bird, though tame, had complete liberty, and being very fond of frogs, it was accustomed to follow its owner, anticipating the amphibian tit-bits which were to be discovered beneath the logs and stones that were overturned for the bird's inspection. But the Seriema was under no misapprehension as to the unpalatability of the black and yellow and scarlet *Phryniscus nigricans*. One look was enough: it could never be induced to have anything to do with this species, which, says Budgett, "at ordinary times is the slowest and most bold of frogs." Charles Darwin also writes * of this species which he observed when visiting Bahia Blanca in 1833:—"Amongst the Batrachian reptiles, I found only one little toad (*Phryniscus nigricans*), which was most singular from its colour. If we imagine, first, that it had been steeped in the blackest ink, and then, when dry, allowed to crawl over a board, freshly painted with the brightest vermilion, so as to colour the soles of its feet and parts of its stomach, a good idea of its appearance will be gained. If it had been an unnamed species, surely it ought to have been called *Diabolicus*, for it is a fit toad to preach in the ear of Eve. Instead of being nocturnal in its habits, as other toads are, and living in damp obscure recesses, it crawls during the heat of the day about the dry sand-hillocks and arid plains. . . ."

The above observations by the herpetologists and field naturalists best qualified to speak on these matters provide a valuable and illuminating contrast to Dr. McAtee's *ex cathedra* pronouncements upon the general inefficiency of the defensive secretions of the Anura, his special pleading that there is lack of evidence for the adaptive significance of colour in frogs, and his confident assertion that discrimination by birds and snakes is a myth!

Dr. McAtee next turns his attention to the adaptations of insects. Commenting upon Swynnerton's experiments (11) which I quoted (pp. 493–4), he once more restates his views on the indiscriminacy of predators, endeavouring to explain away the reluctance of insectivorous animals to eat protected insects as due, not to preference, but to satiety. He says: "A man can eat beefsteak until it palls upon him, but still have an appetite for pastry, and perhaps even for icecream and candy after that. The reverse, however, is just as true, for, granted a fresh start, after being cloyed with candy, he can again relish beefsteak." Now this is all very entertaining, but what does it prove? Does Dr. McAtee believe that a choice of food that is due to satiety disproves the existence of a choice of food that is due to preference? But apart from the bad logic of his argument, the analogy is false,

* *A Naturalist's Voyage*, 1897. London. Chap. V, p. 91.

in that the comestibles which he mentions are all more or less palatable, whereas the insects under consideration are believed by everyone except Dr. McAtee to be relatively unpalatable.

" The whole of the experimental evidence as to edibility of prey," Dr. McAtee tells us, " is scarcely worth the paper it is printed upon, a fact pointed out by McAtee twenty years ago." This is not a fact, but an expression of opinion; and twenty years ago the greater part of the experimental evidence as to edibility was not on paper: nevertheless his statement is not without value, for it enables those who are familiar with the experimental evidence to judge how far they may allow weight to Dr. McAtee's opinion. But I am not quite clear what bearing these pronouncements have upon my paper under review, unless they are intended to distract the readers' attention from the fact that my observations were based not upon experiments, but upon the evidence of stomach-contents of wild animals—a type of evidence which is not open to any of the objections which he raises here. Limitations of space prevent me from referring to more than a few of the remaining fallacies on the same page, where Dr. McAtee's well-known conclusions on availability are given a flourish :—" Animals take what is most available at the particular time and place . . . feeding proceeds from the more to the less available items, not from imaginary preferred or palatable, to the less preferred or unpalatable things. No one who has studied the food habits of wild animals can doubt that availability is in general the controlling factor in the choice of food. . . . There is practically no such distinction as insects good, and not good to eat, for the evidence indicates that all are eaten more or less in proportion to their numbers."

Now what is the evidence? It is typical of Dr. McAtee's methods of criticism that in the course of an extensive review of my paper he makes no mention whatever of the main body of evidence which it contains! In the principal section I dealt with the usefulness of various adaptations in protecting insects against predatory attack by batrachian enemies, as indicated by the stomach contents of 794 tree-frogs. This material was classified in order to show what light the feeding habits of these animals throw upon the relation which is supposed to exist between colour and edibility in insects. Of 10,968 specimens sufficiently complete for analysis, only 14 specimens (·13 per cent.) belonged to the typically aposematic colour group. Not only does he completely ignore these and other facts in my paper which strongly support the theory of warning colours, but Dr. McAtee improves upon the occasion by referring to the evidence here as indicating " practical indiscriminacy."

If Dr. McAtee chooses to turn his back upon all the facts which support the theory of warning coloration, that is his own affair. But his methods of dealing with the evidence demand some comment from those whom he would criticise. Here, as we have seen, his methods are to ignore the facts, to misstate the facts, and to misrepresent the views of those who interpret the facts. As though this were not enough, he further confuses the issue with the introduction of irrelevant matter, with abuse of those with whom he disagrees, and with extravagant speculations upon what their religious views might have been had they lived before the days of Darwin!

The little personal thrusts in his present attack can interest no one except myself. For the rest, the dust of error and misunderstanding which he has stirred up will settle; and with the return of better visibility I cannot do better than commend

Dr. McAtee's review, as to fairness, logic and taste, to the judgment of those whom it may interest.

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Explanation of the Plates.

Plate I.

Rana temporaria Linn. Photograph of the common frog in its natural surroundings, illustrating the combined effect of concealing coloration, obliterative shading and a disruptive pattern, in rendering the animal inconspicuous. From life. Battle, Sussex. Approximately $\frac{1}{2}$ life size.

Plate II.

Bufo typhonius Linn. A leaf-like South American toad which approaches in its form, colour and marking the special protective resemblance to leaves seen in various butterflies, moths, grasshoppers and leaf-insects. From life. Pará, Amazon. Approximately $\frac{2}{3}$ life size.

Plate III.

Fig. i.

A South American tree-frog, showing the procryptic resemblance to bark. From life. Pará, Amazon. The specimen—the only one of its kind that was seen—escaped while being photographed.

Fig. ii.

Hyperolius marmoratus Rapp. A very conspicuous East African Polypedatid tree-frog, wearing a pyjama-like pattern of light-yellow orange-centred stripes alternating with bands of black. From life. Charre, Portuguese East Africa. Approximately $1\frac{2}{3}$ life size.

***Rana temporaria* Linn. Battle, Sussex.**

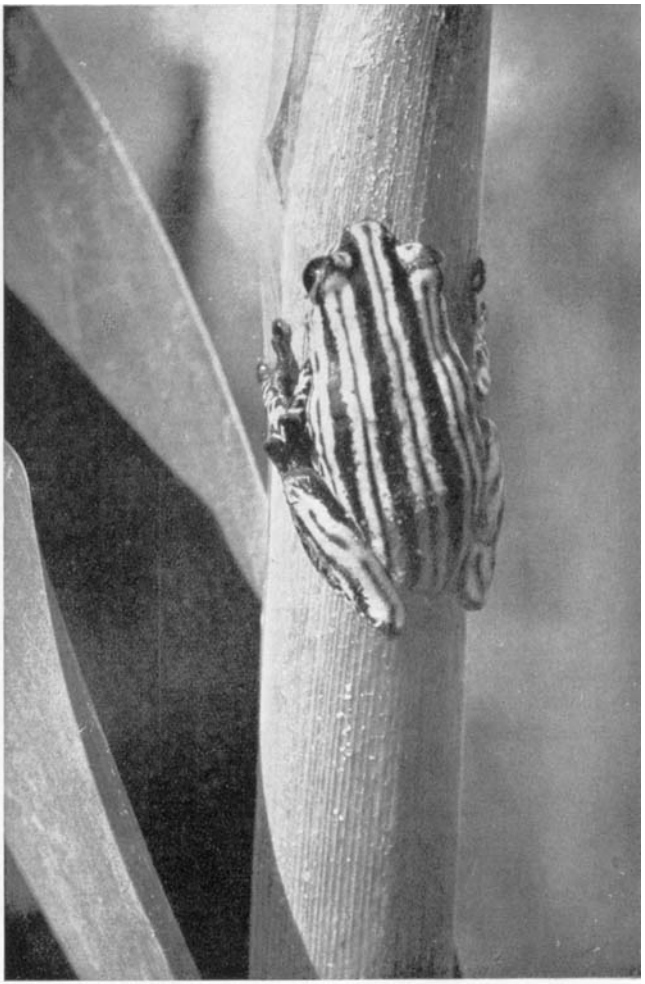
Hugh B. Cott, Photo.

***Bufo typhonius* Linn. Pará.**

Hugh B. Cott, Photo.

Hugh B. Cott, Photo.

Unidentified Tree Frog. Lower Amazon.



Hugh B. Cott, Photo.

Hyperolius marmoratus **Rapp. Portuguese East Africa.**

Hugh B. Cott, Photo.

Chiromantis xerampelina **Peters. Lower Zambesi.**

Hugh B. Cott, Photo.

Phrynomantis bifasciata **Smith. Lower Zambesi.**

Plate IV.

Fig. i.

Chiromantis xerampelina Peters. An East African Polypedatid tree frog, showing procryptic resemblance to bark. From life. Charre, Portuguese East Africa. Approximately $\frac{2}{3}$ life size.

Fig. ii.

Phrynomantis bifasciata Smith. A sluggish aposematic East African Brevicipitid frog, wearing a livery of vermilion and black. From life. Caia, Lower Zambesi. Approximately life size.

Termination of the Controversy with Dr. W. L. McAtee. By Prof. E. B. POULTON.

In a recent paper to which the Registrar directed my attention—"Does 'Protective Coloration' protect—results of some experiments with fishes and birds,"* the author, F. B. Sumner, writes of "the interminable controversy regarding the protective value of animal coloration" (p. 559). Indeed, I fear that to many of our Fellows the discussion must appear well-nigh interminable and that they will welcome its conclusion as heartily as I do. Nevertheless I do not plead guilty to starting it or to entering into it hurriedly. Nearly twenty years passed before I wrote, referring to Dr. W. L. McAtee's first attack,† "I was probably mistaken 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." ‡ The necessary limits imposed upon an address prevented more than a brief statement on that occasion, but in the following year McAtee renewed his attack, in a paper entitled "Effectiveness in Nature of the So-called Protective Adaptations in the Animal Kingdom, chiefly as illustrated by the Food Habits of Nearctic Birds." § To this and his earlier publication, I replied in a paper, read July 1932—"Attempts to disprove the Theories of Warning Colours, Mimicry and Protective Resemblance in Insects." ‖ Dr. F. Morton Jones' important paper, "Insect Coloration and the Relative Acceptability of Insects to Birds," ¶ recording his valuable and careful experiments, was read on 1 June and published in December, 1932, the month during which a discussion on "Protective Adaptations of Animals—especially Insects" was held before our Society (1932 (1933), *Proc. ent. Soc. Lond.*, **7** : 79–105). To this discussion and Dr. Morton Jones' paper, a rejoinder was published by Dr. McAtee in 1933, *Proc. R. ent. Soc. Lond.*, **8** : 113–126, and answered in 1934, *Ibid.*, **9** : 21–40. To these published papers, replies and rejoinders must be added Dr. McAtee's

* 1934, *Proc. nat. Acad. Sci.*, (10) **20** : 559–564. To give an adequate account of this excellent paper would occupy too much space and I must content myself with the author's conclusion from his experiments:—"*It seems evident, in view of all these facts, that fishes which harmonize in shade with their immediate surroundings are less likely to be eaten by birds (or at least by certain birds) than fishes of the same species which do not so harmonize.*" (Author's italics, p. 564.)

† *Proc. Acad. nat. Sci. Philadelphia*, **1912** : 281–364.

‡ "A Hundred Years of Evolution," the Presidential Address to Section D—Zoology, at the Centenary Meeting of the British Association, London, 1931 (*Rep. Brit. Assoc.*, **1931** : 90).

§ 1932, *Smithson. Misc. Coll.*, **85** (No. 7) : 1–201.

‖ 1932 (1933), *Proc. V. Congr. internat. Ent., Paris* : 33–44.

¶ 1932, *Trans. ent. Soc. Lond.*, **80** : 345. The evidence here brought forward is further strengthened by Dr. F. M. Jones' paper, "Further experiments on coloration and relative acceptability of insects to birds," 1934, *Trans. R. ent. Soc. Lond.*, **82** : 443–453, 2 pls.

criticisms answered by Mr. Cott on pp. 109–119, together with the correspondence in *Nature* during 1932.

I have not taken part in this discussion with the slightest hope of convincing Dr. McAtee but in order to guard the reader against accepting his confident assertions and from being misled by his controversial methods. This, I believe, has been sufficiently accomplished and I do not propose to continue the discussion with him, a decision which has been confirmed by the opinion of my friend Dr. F. Morton Jones, who wrote on 29 Sept. 1934 :—

" I think you are right that continued controversy which leaves the participants still of the same opinion and which takes up so much time and space, is unprofitable. Certainly the accumulation of evidence from every possible viewpoint, will have more permanent value. Obviously, we have not passed that stage yet, in the study of the significance of insect habit, structure, and coloration."

Apart from the discussion here referred to, Dr. McAtee's disparaging references to " Selectionists " suggest that he belongs to the Neo-Lamarckian school, powerfully represented in America half a century ago. I recall many keen but pleasant encounters with American comrades, and especially with my dear friend Prof. Fairfield Osborn at the 1888 meeting of the British Association in Bath, when we argued so far into the hours which should have been devoted to sleep that we found ourselves seriously debating how far an absolutely sterile hybrid could transmit qualities to its descendants ! However, the teachings of Weismann did not take long to soak in, and when Mendelian heredity was rediscovered Lamarckism received another tremendous blow. Although this great rediscovery was at first hailed as the end of Darwinian evolution by Natural Selection, further researches, chiefly by American zoologists, led to very different conclusions, as Prof. H. S. Jennings stated in 1917 :—" Evolution, according to the typical Darwinian scheme, through the occurrence of many small variations and their guidance by natural selection, is perfectly consistent with what experimental and palaeontological studies show us "; appearing indeed to the author to be " more consistent with the data than . . . any other theory." *

The termination of this controversy does not by any means imply, as Dr. Morton Jones has pointed out above, any cessation in " the accumulation of evidence from every possible viewpoint . . . in the study of the significance of insect habit, structure, and coloration." In order to realise the fundamental importance of this evidence we only need to recall H. W. Bates' words on p. 511 of his classical paper † :—" The process by which a mimetic analogy is brought about in nature is a problem which involves that of all species and all adaptations."

* See *Proc. ent. Soc. Lond.*, **1917** : lxxxv, for amplification and references; also *Rep. Brit. Assoc.*, **1931** : 76, 77, reprinted as No. 2 in 1933, *Hope Reports*, **19**. See also S. E. [C.] Harland, on " The Genetic Conception of the Species," in *C. R. Acad. Sci. U.S.S.R.*, **1933** : 181–186.

† 1862, *Trans. linn. Soc.* (*Zool.*), **23** : 495.